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DOUBLED CHROMOSOMES OF OENOTHERA LAMARCKIANA SEMIGIGAS

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(WITH TWO FIGURES)

Introduction

In a previous paper (8) we have tried to show that the numerous types of the mutants of *Oenothera Lamarckiana* may be combined into groups. We started from two principles: the frequently repeated production of one type by another, and the striking external resemblance of forms which were different in their hereditary features. *O.* mut. *albida* is produced almost yearly by *O.* mut. *lata*, and in a relatively high percentage. *O.* mut. *oblonga* almost always is seen in large numbers among the progeny of *O. scintillans*. It is evident that such repeated productions point to some kind of intimate connection, such as can be explained only on the assumption that the factors for the two types are located in the same chromosome. On the other hand, in all its organs *O.* mut. *nitens* shows the same characters as *O.* mut. *scintillans*, although the first type is constant, whereas the other splits, in each generation, into specimens of its own form and others of the type of *O. Lamarckiana*. The external features being the same for both, their factors must also be assumed to be the same, at least mainly. *O.* mut. *nitens* and *O.* mut. *scintillans*, therefore, were assumed to be located in the same chromosome.

Applying these principles to the great majority of the mutants, we had seven groups, corresponding to the seven chromosomes of the haploid nucleus. One of them consisted chiefly of the isogamic mutants, but in each of the others one of the dimorphic or splitting mutants prevailed. Accordingly we proposed to call the chromosomes after these. The name of central chromosome was chosen for the one containing mainly isogamic types, and two of the others were called after *O.* mut. *lata* and *O.* mut. *scintillans*, reserving the names of *cana*, *pallescens*, *liquida*, and *spathulata* for the four remaining ones. The three first groups were found to be large; they may correspond to the three large chromosomes described and figured by CLELAND for *O. franciscana* (2). The four other groups would then correspond to the four smaller chromosomes of the haploid nucleus. We have since found these small and large chromosomes in the nucleus of *O. Lamarckiana* itself.

It is well known that the heterogamic mutations of *O. Lamarckiana* as a rule are connected with the doubling of one of the chromosomes. This brings their number in the vegetative cells up to 15. Why this should be so we do not know, since the doubling may be accompanied, for each chromosome, with widely different types of mutations, such as *albida* and *lata* in one case, or *oblonga* and *scintillans* in another. Moreover, the hereditary features are not determined by this doubling, since in almost every group *sesquiplex* or constant forms are found besides the typical dimorphic or splitting ones. The connection is such, however, that in ordinary cases one may confidently rely upon it for conclusions.

It would follow that the progeny of mutants of the type of *semigigas* might afford a good test for our conceptions. It is astonishingly rich in forms, some of which repeat the old types (*O. lata*, *O. scintillans*, and *O. oblonga*) in a relatively high percentage, whereas others constitute new types occurring in smaller numbers or even in single individuals, as has been described by one of us (4). At that time (1913), however, only three of the dimorphic prototypes (*O. lata*, *O. scintillans*, and *O. spathulata*) had been discovered, and thus the principle for grouping the numerous forms failed. *O. cana*, *O. pallescens*, and *O. liquida* have since been distinguished (5), completing the series. If we

apply these forms as models for distinction to the motley progeny of *semigigas*, the main groups at once become prominent. Besides *lata* and *scintillans*, which are always easily recognized, *cana* and *spathulata* become evident, and *pallescens* and *liquida* can also be distinguished, although not with the same clearness. In some specimens these types seemed to be as pure as those of the corresponding old races, but in many others they were evidently obscured by subordinate deviating characters.

From numerous cultures of the progeny of different types of *semigigas*, we discovered that the clearness of the groups depends largely on the choice of the type which yields the pollen for the fertilization. In order to get a sufficient supply of good seeds the flowers of *semigigas* have to be fecundated by means of other pollen; self-fertilization produces too few germinating seeds. Some pollen proved to be dominant over a majority of the mutations, making the distinction very difficult and in some degree uncertain (as that of *O. Lamarckiana* mut. *gigas*); other types proved to be recessive, allowing a clear grouping. Among these, the forms of *velutina* were the most reliable.

For this reason we have chosen for the present investigation the pollen of the twin hybrid *O.* (*biennis*×*Lamarckiana*) *velutina*. There are many mutants, especially among the *sesquiplex* types, which yield sufficiently pure *velutina* pollen (**6**), and some of them have been used for control experiments, as will be shown elsewhere. The twin hybrids of *O. Lamarckiana* are old forms described since 1907, however, and studied by many investigators. Moreover, they easily may be reproduced by anyone interested in the present discussion.

Oenothera (lata×Lamarckiana) semigigas

In 1915 a mutant *lata* originated from the pure race of *O. Lamarckiana*, and was chosen for the production of a new line. Every generation of this line has been fertilized by the pollen of *O. Lamarckiana*, since the *lata* plants had no good pollen, as is usual in our climate. In the third generation, in 1921, two rosettes of the type of *semigigas* were observed. The chromosomes in the root-tips of both of them were counted and found to be 21. The

plants remained in the condition of rosettes of leaves until the winter, and flowered in 1922, when they were used for this experiment. They were cultivated in the glass covered part of the experiment garden at Lunteren, under very favorable conditions, and flowered richly. On one of them thirty flowers of the side branches were pollinated, after a castration, with the pollen of *O.* (*biennis*×*Lamarckiana*) *velutina*. They yielded 30 apparently good fruits, with 3.3 cc. of seeds, about one-quarter of which contained viable germs, as was proved in a test-tube at 30° C. The other seeds had imperfect germs of different sizes.

The harvest was sown at the end of January, 1923, in a glass-house, and 81 seeds germinated. The young seedlings showed a motley assembly of types of leaves, among which some were more frequent and could soon be recognized. After two months they were transplanted singly into small pots, and from these they were planted in the beds, in May and June, as soon as their root tips had been fixed for the counting of chromosomes. At that time the mutant characters could be recognized clearly in most of the rosettes of root leaves, and the plants were grouped accordingly before being planted. This method has the advantage that, at the time of flowering, the mutants belonging to the same type were side by side. Thus the different groups could easily be distinguished, and also the slight deviations in the individual characters within each group could be subjected to a careful comparative study. Most of the 81 mutants flowered during July and August, and ripened their fruits in the fall. They were stout, healthy plants, whose characters could be compared with those of the older mutant races, all of which flowered at the same time in the experimental garden.

This comparison was begun in the stage of rosettes and continued through the summer, until the ripening of the fruits. As a rule the rosettes show their type distinctly at the time of planting, or, on weaker plants, some weeks later. Then the young stems develop with a less differentiated foliage, but the spikes of flower buds are seen to develop once more the marks of the groups. Moreover, the deviations from the main types are usually small during youth, but become more pronounced with advancing age.

This article reports only the results of the cross *semigigas*×*velutina*. The reciprocal cross would not produce a similar deformity. We may conclude this from a study of the effect of the pollen of our plant in other different crosses, made in 1922, partly on other species, partly on the parent type and some of its mutants. For each of these crosses 10–15 or more flowers were pollinated, and yielded 40–60 or more viable seeds. In May the rosettes had reached the stage in which the marks of *laeta* and *velutina* are easily distinguished, but no *velutina* were found. Thereupon 12 specimens from each cross were planted out and cultivated during the whole summer, until they began to ripen their seeds. In the crosses with *O. biennis*, *O. grandiflora*, and *O. blandina* they were exactly like the *laeta* from the corresponding crosses with *Lamarckiana*. In *Lamarckiana*×*semigigas* they repeated the marks of the mother, and in *lata*×*semigigas* they were partly *lata* and partly *Lamarckiana*. No other types were observed in these cultures, which embraced in all over 400 rosettes and 60 flowering plants. The high degree of mutability, shown by the cultures derived from the egg cells of *semigigas*, failed in those from the pollen. From this experiment, therefore, we conclude that the pollen of our *semigigas* contains, among its viable gametes, only or almost only such of a sufficiently pure *laeta* type.

Doubling of chromosomes

Stomps (**11, 12**) was the first to introduce the study of *O.* mut. *semigigas* into the discussion concerning the stage at which the doubling of the chromosomes takes place. He counted its chromosomes and found them to be 21. From this he concluded that the doubling must occur in the production of the sexual cells before fecundation. The *semigigas* would then originate by the fertilization of a doubled gamete by a normal one, whereas the conjugation of two doubled ones would yield a *gigas*. This conception has since been generally accepted, although it was in flagrant contradiction with the older view of a doubling after fertilization, as had been proposed by Strasburger. Ernst (**9**) has formulated the theory of Stomps clearly, stating that in the production of the mother cells of the pollen and the embryo sac, the reduction division is sometimes

omitted. This, of course, must be a rare phenomenon, and may be considered the consequence of some internal mutation.

On the basis of this view, the term doubling is rather a misleading one. In the process of synapsis the chromosomes conjugate, and at the time of the reduction division they quit each other. If this latter event is omitted, they must remain in the combined condition at least for some time, and thus cause the image of a doubling; and if this doubling is considered to be a phenomenon of mutation, we must assume that the separation of the paired chromosomes in reduction is determined by some special factor, which may become inactive in rare instances and from an unknown cause, thus producing the mutation. This view is a direct consequence from the theory of STOMPS, and is interesting for our present discussion, inasmuch as it throws light on the relation between the process of doubling and the external mutations which ordinarily accompany it. This relation cannot be considered a causal one, but only one of binding or linkage. In the description of our experiment we shall find some direct proofs for this conception (*O. Lamarckiana* with 15 and 20 chromosomes).

In the synapsis of *semigigas*, the doubled chromosomes are paired with the single ones, and during reduction they separate, and one of each pair goes to one pole and the other to the second pole. STRASBURGER pointed out that in this process the distribution of the chromosomes depends upon chance. One nucleus will receive a larger number of rods from the maternal group, and another more from the paternal, and many may have equal groups of both. ZIEGLER (13) then applied to this conception the laws of probability, showing that the distribution must proceed according to these. Applying this principle to the case of *semigigas*, we should expect its doubled chromosomes to be distributed among the egg cells according to chance.

This conclusion has been tested by VAN OVEREEM for the case of *O. Lamarckiana semigigas* on the individuals of this form which had arisen in the cultures of one of the writers in 1913. When this mutant is fertilized with the pollen of *O. gigas*, almost all the seeds are viable, or at least a sufficient part of them, and the numbers of the chromosomes may be expected to lie between 21 and 28, indicat-

ing 7 and 14 doubled ones. If an egg cell of *semigigas* without such is fertilized, the germ will have 7 single and 7 doubled ones, and $7+14=21$ rods will be counted in the nuclei. If, however, egg cells whose chromosomes are all doubled are considered, there will be two sets of 7 doubled ones, giving together 28 visible rods. From the numbers given by VAN OVEREEM, the numbers of double rods in *semigigas* may be calculated after this rule. He found for this cross, among 87 seedlings:

Chromosomes.....	21	22	23	24	25	26	27	28
Number of seedlings.....	1	2	12	21	25	19	6	1

This gives for the number of doubled chromosomes in the egg cells the same numbers:

Doubled rods.....	0	1	2	3	4	5	6	7
Egg cells.....	1	2	12	21	25	19	6	1

The number of possible cases in this row being 8, we chose for the calculation of the chances the curve corresponding to $(a+b)^7$. The height of the ordinates of this curve is proportional to $1.7.21.35.35.21.7.1$. The sum of these numbers being 128, and that of the seedlings 87, we must multiply the latter by $128/87$ in order to compare them. Assuming further that the empirical curve should be symmetrical, we calculate the means between its two halves. In this way we have:

DOUBLE CHROMOSOMES IN THE EGG CELLS OF *O. semigigas*

Chromosomes.....	0	1	2	3	4	5	6	7
Egg cells calculated.....	2	3	17	31	37	28	9	2
Eggs calculated symmetrically...	2	6	22	34	34	22	6	2
$(a+b)^7$.....	1	7	21	35	35	21	7	1

The coincidence is as close as could be expected, and shows that in the reduction division of *O. semigigas* the doubled chromosomes are distributed among the two daughter nuclei according to the laws of chance.

A main condition in this discussion has been that all or almost all the seeds are viable. If this is not so, the result may be different. In the case of *semigigas*×*velutina*, only about one-quarter of the seeds were well developed, and the question arises, what influence this may have on the figures. In order to answer this, we assume that in our case the simultaneous occurrence of two or more

doubled rods in the nuclei of a seedling is detrimental for its development. The doubling is assumed to be connected with the same mutations of the normal characters with which it is connected in the old heterogamic races, and these mutations are probably more or less incompatible with one another. We may conclude this from the fact that mutations with 15 chromosomes, that is, with one doubled rod, are frequent, whereas those with 16–20 chromosomes as yet have not or almost not been discovered outside of the progeny of *semigigas*. Their chance of survival, therefore, must be very small; most of them, when produced in the germ, must be lost before the ripening of the seed.

As yet there is no reason to assume a lessened viability for plants with only one doubled rod. They must be as good, in this respect, as the normal races with 15 chromosomes. This leads us to expect a high proportion of seedlings with this number, and gradually smaller figures for those with more chromosomes.

NUMBER OF DOUBLE CHROMOSOMES AMONG PROGENY OF OENOTHERA (LATA×LAMARCKIANA) SEMIGIGAS

Our culture embraced 81 seedlings, which were planted singly in small pots as early after germination as possible. As soon as a sufficient number of root leaves had developed, root tips were prepared, and thereupon the young plants were placed in the beds of the glass covered part of the garden, without their pots. Their development differed very much in rapidity; accordingly the fixation was performed at different times in May and June, 1923.

The fixations were made early in the morning, using BOUIN'S fluid. The preparations measured 5–10 μ, mostly 10 μ, in thickness, and were stained with the haematoxylin solution of Haidenhain. The general results of the counting were as follows:

Chromosomes	14	15	16	17	18	19	20
Number of plants	3	35	19	13	3	4	4

These numbers yield an asymmetrical curve, as is shown in fig. 1. The explanation of the asymmetrical form of the curve depends on the assumption that the chance of viability became smaller with an increasing number of double chromosomes. In this respect the result of the fertilization of *semigigas* with pollen of

velutina would differ essentially from that with pollen of *O. gigas*. It is interesting to note, therefore, that even in the living seedlings the chances are better, the fewer the number of double rods. This may be proved by comparing the degree of development, attained before the fall of the first year, with the numbers of such bodies.

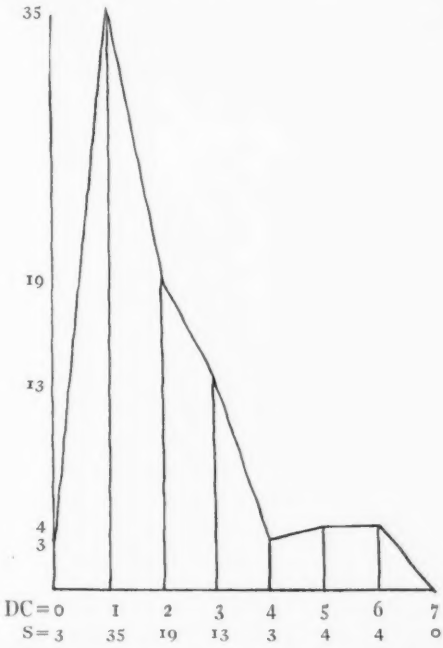

FIG. 1.—Numbers of chromosomes in seedlings of *Oenothera* (*lata*×*Lamarckiana*) *semigigas*×*O.* (*biennis*×*Lamarckiana*) *velutina*; *DC*, doubled chromosomes; *S*, seedlings.

Among the 81 plants, 12 remained in the stage of rosettes (one of them died before the fall, being very weak); 9 made a stem, but did not reach the flowering period; 13 flowered, but had barren anthers, at least in the beginning; and only 47 developed throughout in a normal way. If we consider these four groups as a measure of the individual strength, and compare them with the numbers of chromosomes, we get the data given in table I.

In order to get an easier survey we combine the figures into groups, and calculate their percentages (table II). This table shows that the larger part of the normal plants had 14–15 chromosomes, whereas the rosettes had mostly an abnormally high number. In other words, the development is the more incomplete, the larger the number of mutated chromosomes. From this we may safely conclude that among the sterile seeds the high chromosome numbers

TABLE I

FALL OF 1923

	Number of doubled chromosomes						
	0	1	2	3	4	5	6
Rosettes	0	0	4	3	3	1	1
Young stems	0	2	2	3	0	2	0
Barren anthers	0	4	6	2	0	1	0
Normal plants	3	29	7	5	0	0	3
Total	3	35	19	13	3	4	4

TABLE II

PERCENTAGES OF CHROMOSOMES

	Number of chromosomes		
	14–15	16	17–20
Rosettes	0	33	67
Young stems	22	22	56
Barren anthers	31	46	23
Normal plants	68	15	17

must prevail, leaving only a small proportion for the viable germs, and this is sufficient proof for the validity of the assumption just made.

CHROMOSOMES AND EXTERNAL FEATURES

In studying the progeny of another form of *semigigas*, one of the writers found that the offspring may be combined into groups, and that the majority of these correspond to the dimorphic mutants previously described (7). *O.* (*blandina*×*simplex*) *semigigas* (*O. perennis*) was fertilized, partly with pollen of other species, partly with that of different mutants of *O. Lamarckiana*, and the progeny

counted at the time of flowering. Six main groups were distinguished, corresponding to the old dimorphic races, and among these there were about 8 per cent *lata*, 36 per cent *scintillans*, 11 per cent *cana*, 8 per cent *pallescens*, 4 per cent *liquida*, and 4 per cent *spathulata*. Of course, the figures are only approximate, since a large part of the plants did not reach the period of flowering, but it should be noted that the size of five of these groups lies between 4 and 11 per cent, whereas only one, that of *scintillans*, is seen to differ widely. The kind of pollen used for the crosses did not seem to have a notable influence on the numerical relations between these divisions.

Combining this result with our hypothesis concerning the distribution of the mutant characters among the six lateral chromosomes of the haploid nucleus (**8**), we find an exact correspondence in the main points, but it seemed desirable to give further proofs and to study these relations in more detail.

We shall first give a survey of the groups concerned, and discuss the individual deviations afterward. We call prototypes the forms of the old races, which served for comparison. It should be remarked that the mutants of our experiment cannot be expected to be exactly the same as these prototypes, since their male parent was always the *velutina*. In the prototypes the paternal half of the nucleus is *velutina* only in the sesquiplex mutants *oblonga*, *auricula*, and *candicans*, but *laeta* in the dimorphic races (*lata*, *scintillans*, *cana*, *pallescens*, *liquida*, and *spathulata*). This causes some differences, especially in the leaves, which are broader for *lata* and narrower for *velutina*. In some instances this difference is striking, but in others it is very small, as in the case of *O. cana*.

The isogamic mutants *nanella* and *rubrinervis* have not been observed in our culture; no dwarfish or brittle specimens were seen. Some plants were like *Lamarckiana*, and others constituted a new type, which was almost like the parent species, but reached only half its height. We call it *O. Lamarckiana* mut. *pulla* (fig. 2). Two plants repeated the features of *O. Lamarckiana* mut. *hamata*, a race cultivated since 1918, but as yet not published. The vast majority of the mutants showed more or less clearly the types of our old dimorphic races. Table III gives the prototypes represented in the numbers of individuals.

From table III we see that the dimorphic races, with the exception of *lata* and *cana*, were represented in high and almost equal numbers (10–13.5 per cent), whereas the secondary types were present in only one or two specimens each. There are seven main groups, including *lata* but omitting *Lamarckiana*, and this points to the conception that each of them corresponds to one of the seven chromosomes of the haploid nucleus.

If we apply the law of probability not only to the numbers of the chromosomes, but also to their qualities, we may consider it very probable that the different chromosomes will be equally represented among the different groups of seedlings. Thus we should

TABLE III

GROUPS ACCORDING TO PROTOTYPES

Prototypes	Number	Percentage
lata	2	2.5
scintillans	10	12.5
oblonga	1	1.3
auricula	2	2.5
cana	18	22.5
candicans	1	1.3
pallescens	8	10.0
liquida	9	11.3
spathulata	11	13.5
hamata	2	2.5
pulla	10	12.5
Lamarckiana	6	7.5
Total	80	.....

expect seven main groups of mutant characters to be represented with about equal frequency, each corresponding to the doubling of a distinct nuclear rod. The expected groups would then correspond to the observed ones. Why the type of *lata* should be rarer and that of *cana* more frequent remains obscure. In this respect, however, it should be remembered that among the progeny of *O. perennis* (*O. blandina*×*simplex*) *semigigas*, another group, that of the type of *scintillans*, is in the majority, a fact which obviously diminishes the importance of such deviations. From this we may infer that the different chromosomes are the bearers of distinct groups of mutant characters, or, in other words, that each chromosome is the bearer of the factors of one of the seven main types of table III. This conclusion is in harmony with the hypothesis of

the distribution of mutant characters among the chromosomes, and may be considered to offer a new proof for it. Moreover, in their main features the groups are the same as those described for *O. perennis*.

Table IV gives the number of chromosomes for the constituents of these different groups. It is to be remarked that one of the 81 plants (one with 17 chromosomes) died in early youth, before developing its character. All the others reached the fall, mostly in flowering condition, but partly as rosettes or young stems.

In almost every group at least one of the chromosomes is doubled, and the doubling of two or more such bodies, taken

TABLE IV

MUTANTS OF *O. semigigas—velutina*

Prototypes	Number of chromosomes						
	14	15	16	17	18	19	20
lata	.....	1	.....	1	.....	.....	.....
scintillans	.....	2	3	2	2	1	.....
oblonga	.....	1	.....	.....	.....	.....	.....
auricula	.....	1	.....	1	.....	.....	.....
cana	.....	10	3	3	.....	1	1
candicans	.....	.....	1	.....	.....	.....	.....
pallescens	.....	1	3	1	.....	2	1
liquida	.....	7	2	.....	.....	.....	.....
spathulata	.....	4	4	2	1	.....	.....
hamata	.....	2	.....	.....	.....	.....	.....
pulla (fig. 2)	.....	5	3	2	.....	.....	.....
Lamarckiana	3	1	.....	.....	.....	.....	2

broadly, is equally distributed among them. From this we may conclude that the external features of the types as a rule are connected with the doubling of one chromosome in each case, but that the doubling of the others is of secondary importance. It produces, or is related to, small deviations from the prototype, but does not essentially change it. We may assume that in every case the factors of one chromosome are dominant over those of the others, but why in one case this chromosome should prevail, and others in other cases, we do not know. This condition, however, obviously runs parallel with the well known fact that the parent species produces in some instances a *lata*, in others a *scintillans* or a *cana*, and this without the slightest indication of the cause of such a choice.

In every group two main causes of individual differences are to be considered. One of them is connected with the doubling of more than one chromosome, and it is usually assumed that factors of the other doubled ones are influencing the visible features of the plants. Even if only one chromosome is doubled, however, our plants may show deviations from their prototype, and in such cases we must suppose that in the same rod different groups of factors have become mutated.

Pure types have occurred in our experiment only in specimens having one rod doubled, as will be seen in table V. In this table

TABLE V

PURE AND DEVIATING TYPES OF MUTANTS

PROTOTYPES	15 CHROMOSOMES		16–20 CHROMOSOMES	
	Pure	Deviating	Pure	Deviating
lata	.....	1	.....	1
scintillans	2	.....	.....	4
cana	8	2	.....	5
pallescens	.....	.....	.....	5
liquida	7	.....	.....	2
spathulata	4	.....	.....	(0)

only the flowering plants are mentioned, but it is to be remarked that for *spathulata* 6 specimens which did not produce flowers could be added to the last column. The specimens of *oblonga*, *auricula*, *candicans*, and *hamata* were sufficiently pure to their types, and of the *pulla*, for which no prototype is as yet known, all had the same form, with only one exception (with 16 chromosomes). It must be remarked, however, that numerical relations of this kind are very changeable among the progeny of *semigigas*, and that other crosses of it have given different results. It is, therefore, only on the main points that we wish to lay stress. Numerous types may lay hidden in the germs of the non-germinating seeds.

CHARACTERS OF MUTANTS

The different forms of mutants seen in our cultures will be described, beginning with the largest group, the *cana*-like plants. It is at the same time the most complete, and the incompleteness of the other groups may therefore be ascribed to their smallness.

PROTOTYPE *cana*.—Seven plants were exactly like the race of this name, which has been described by one of the writers (5), and of which the fourth generation flowered in 1923 in the experimental garden in 6 pure specimens. The likeness was already evident in the rosettes, and the 7 plants were planted in a row. By this means their uniformity was made very striking. The spikes are long and thin, with long internodes, narrow bracts, long thin flower buds, and thin cylindrical fruits. All organs are grayish. The flowers are almost erect, and the calyx tube is correspondingly bent. The petals spread only halfway. The tips of the calyx are bent sideways in the plane of symmetry of the buds, pointing outward in respect to the spike. All of the seven specimens reached the same height, which in mid August reached 1–1.25 m. They were richly branched. They only differed from the old race in somewhat narrower leaves and bracts, and slightly more compact flower buds, as was to be expected from the influence of their *velutina* parent. Among the deviating plants of this group two specimens with 15 chromosomes differed only in being weaker, reaching about one-half the height of the others, and in having thicker fruits, which were almost like those of *O. Lamarckiana*.

The three specimens of *cana* with 16 chromosomes hardly differed from the main type. Two of them had broader leaves, especially in the rosettes, the fruits being *cana*-like in one of them and *Lamarckiana*-like in the other. The third plant developed its grayish color relatively late in the spring. Their flowering spikes were as described, with the exception that the anthers of one specimen were almost barren. The two plants with 17 and 19 chromosomes were also evidently *cana*, one with broader and one with narrower leaves, and both with smaller and stouter flower buds. They were weak plants, which opened their first flowers only in the last days of August. Three specimens of the *cana* type stayed in the condition of rosettes.

There was one *candicans* among the plants. In early youth the race of this name is almost exactly like *cana*, and so this plant was considered to belong to this type until it developed its flowering spike, which proved it to be a *candicans*. Differences between this specimen and the race have not been noticed.

PROTOTYPE *lata*.—There were only two plants belonging to this type, one with 15 and one with 17 chromosomes. Both differed in many points from the pattern, as in having stout stems and shorter leaves. They did not reach the flowering period before the fall, and were mainly recognized by the dense grouping of their young leaves, so characteristic for *lata*.

PROTOTYPE *scintillans*.—In 1923 we had a large bed of *scintillans* ×*blandina* in order to compare the mutants with this hybrid. The cross had been made in 1919, and the culture of 1923 was the second generation, which embraced about 20 specimens of the type of *scintillans*, with the same dark green and shining leaves, but considerably narrower than those of the race. This was especially evident during the period of the rosettes, and at this time four of the mutants were exactly like the hybrid prototype, which carried the characters of *O. Lamarckiana* mut. *velutina* (*O. blandina*) in the paternal halves of their nuclei. Of these four mutants, two had 15 chromosomes and the two others 17. The two first remained true to their hybrid pattern during their whole life, but of the two latter one distinguished itself at the flowering period by a broader foliage. The fourth one stayed in the condition of a rosette until the fall.

Among the remaining six specimens, three were narrow leaved and three broad leaved in comparison with the typical ones. The first had 16, 18, and 19 chromosomes, and the latter 16, 16, and 18. Sundry smaller differences were observed among them, as was to be expected, but the main type was in every case that of the group. One narrow leaved and one broad leaved plant have not succeeded in developing a stem in the first year (chromosomes 18 and 19).

One specimen of *oblonga* occurred. It was easily recognized when still very young, and remained throughout life true to its type. Of *auricula*, two specimens were observed (with 15 and 17 chromosomes). We had a culture of 16 flowering plants of the fourth generation of the race of that name for comparison. The rosettes are easily confused with those of *cana*, but the stout stems, large flower buds, and broad fruits cannot leave any doubt. Differences between the two mutants and the race have not been observed.

PROTOTYPE *pallescens*.—Only one plant of this group had 15 chromosomes. It was almost like the normal race, but had somewhat broader leaves, especially in its youth. Three specimens

had 16 chromosomes, one of them remained a rosette, whereas the two others flowered but produced hardly any pollen. The same condition prevailed for a plant with 17 and another with 19 chromosomes, and another plant with the latter number did not flower. Among the flowering plants of this group a curious deviation occurred more or less often, consisting in swollen stigma lobes which broadened the tops of the flower buds before opening. One plant with 20 chromosomes was free from this disease, and produced enough pollen for self-fertilization. It, however, had long, very narrow, and almost linear leaves.

PROTOTYPE *liquida*.—The plants of this group constituted a very uniform type, which could be compared with a culture of *O. liquida*×*Lamarckiana* mut. *velutina*, and was found to be almost identical with it, in the rosette stage as well as during the period of flowering. The root leaves are lanceolate, longer and narrower than those of the pure race of *liquida*, and pressed to the ground so as to form a dense rosette. The flower spikes were dense like those of the race, with numerous long and somewhat thin buds and stout fruits. In the culture of the race of *liquida* outside of the glass covered part of the garden the color was brownish, but in a specimen in that part and in the mutants the young organs were almost a pure green. Seven of the plants had only one chromosome doubled; in the two other plants two nuclear rods were in this condition. One of them did not produce a stem; it had long petioles and very pointed leaf blades; the other was almost equal to the typical specimens of the group. On the flowering plants the pollen was abundant, and artificial fertilization was always easy and successful.

PROTOTYPE *spathulata*.—Almost circular leaf blades on long and erect petioles are characteristic of this group during the stage of rosettes, and make it easily recognizable. This type of leaves is followed by the spathulate form as soon as the stem begins to develop. In the individuals with 15 chromosomes the root leaves were pale green; in the others they had a darker tinge and were usually more or less bent against the soil. As a rule the plants in this group were weak. Only those four which had 15 chromosomes flowered, but none of them has produced sufficient pollen for artificial self-fertilization. Among those with 16, 17, and 18 nuclear

rods, three could produce only low stems and four remained in the condition of rosettes.

In the outward features of their inflorescences, the four plants with the normal number of chromosomes were almost exactly like the specimens of the pure race of *O. spathulata*. We also had a

FIG. 2.—*Oenothera Lamarckiana* mut. *pulla;* photograph by M. STAKMAN.

biennal plant of *spathulata*×*blandina*, which flowered richly, but did not show striking differences from the pure mutant.

The two plants of *hamata* were only recognized as such at the time of flowering, and could be compared with 15 typical specimens of the fifth generation of the pure, dimorphic race of the same name. No real differences were observed.

TYPE *pulla* (fig. 2).—Of the ten plants of this form, nine were almost exactly alike, with a very typical form of the radical leaves and the same stem and spike reaching the same height at the time of flowering, in the middle of August. One specimen with 16 chromosomes slightly deviated in its characters; moreover, it did not produce any good pollen, whereas all the others were rich in this respect. It was also weaker and of lower stature. The main form reached about one-half the height of the normal *Lamarckiana*, and had the same stature as this, with a more condensed spike and a less branched stem. Of all the mutants, the *pulla* differed the least from *O. Lamarckiana*. The flower buds reached the same size, although they were not as completely filled. The fruits were as broad and stout, and as rich in seeds as those of the parent species. In the spring the radical leaves of this form had been quite a puzzle, since the type was unknown at that time. These leaves resembled those of *O. gigas* in being broad, with a rounded tip and a sharp contraction of the bases, which separated the blade from the long and winged petiole. They were given a special name, but proved later to correspond to the type now called *pulla*.

On account of the small and hardly striking differences from the parent species, we assume that the factors of *pulla* are to be sought for in the same chromosome which decides the main characters of *O. Lamarckiana* itself, bearing the determiners for *laeta* in some of the gametes and those for *velutina* in others. We have called this chromosome the central one, but the outward features of *pulla* are accompanied by a doubling of one of the nuclear rods. Five specimens had 15 chromosomes, whereas three had 16, and two 17 such bodies. The mutations previously ascribed to the central chromosome, such as dwarfishness and brittleness, are not accompanied by an increase of the number of nuclear rods. If our conception is true, the *pulla* completes the series of the seven cases of chromatic doubling which must cooperate in the formation of *semigigas*. From this point of view it is interesting to note that the *pulla* occurred in about the same number of individuals (12.5 per cent) as most of the other main types of mutations.

Lamarckiana-LIKE PLANTS.—In the reduction division of *semigigas*, the extreme case is that the seven doubled chromosomes

go to one gamete and the seven single ones to the other. After fertilization with *O.* (*biennis*×*Lamarckiana*) *velutina* the first group would produce germs with 21, but the other group would give embryos with 14 nuclear rods. Those with 21 would constitute *semigigas* plants, but their chance of survival is small, and in our experiment such individuals have not occurred. Those with 14 chromosomes would give pure or almost pure *Lamarckiana*, provided their maternal gamete belonged to the *laeta* type. Such is probably the case at least in a sufficient number of germs, as we have previously seen in the crosses of the pollen of *semigigas*.

In the culture of the progeny of *semigigas*×*velutina*, three plants were found with 14 chromosomes and the external marks of *O. Lamarckiana*, corresponding to the expectation derived from this discussion. The rosettes were very stout and easily recognized, almost all the others being much weaker. In the flowering condition the stems were as high and as stout as in the species itself, but the flowers showed some influence of the characters of their grandparent *O. biennis*, as was to be expected. The flower buds were somewhat more cylindrical and the petals smaller than in the pure *Lamarckiana*. For the same reason the spikes were more compact and the bracts smaller, but the differences were very small and did not essentially lessen the resemblance to ordinary *Lamarckiana*.

Moreover, there were two plants with the same stature and external marks, which, however, had 15 and 20 chromosomes. In these cases the doubling of the chromosomes was not followed by the visible mutations which otherwise always seem to accompany it, proving once more that this combination is not a necessary one. Another plant with 20 chromosomes had very long, almost linear leaves, constituting a type of its own of very doubtful interpretation. The linear form of the leaves, however, although not at all rare among the progeny of *semigigas*, does almost always obscure the other marks.

Summary

1. The progeny of *Oenothera* (*lata*×*Lamarckiana*) *semigigas*× *velutina* constitutes a motley assembly of forms, many of which are already recognizable among the young seedlings. On the

contrary, the hybrids, produced by means of the pollen of *semigigas*, did not show any noticeable variability.

2. In the first named cross the mutants belong to different groups, corresponding to the older mutant races derived from *O. Lamarckiana*. There are seven main types, of which six are those of the dimorphic (heterogamous and splitting) mutants *lata*, *scintillans*, *cana*, *pallescens*, *liquida*, and *spathulata*, while one constitutes a new type (*O.* mut. *pulla*). With the exception of *lata* and *cana*, these groups occurred with almost the same frequency.

3. Besides these main forms, single plants of secondary types were observed. They were one *oblonga*, two *auricula*, one *candicans*, and two *hamata*.

4. In almost one-half of the mutants (35 individuals out of 81) the number of chromosomes was 15, or the same as in the older heterogamic mutant races. As a rule, these plants showed all the marks of those races, although, on account of their *velutina* gametes, they could not be expected to be identical with them.

5. In the other half of the mutants the chromosome numbers were 16–20, and the external features were correspondingly mixed, but almost always one of the main types could be recognized as the prevailing one.

6. The 15 chromosome offspring of *semigigas* belong to different types. Among these some are frequent and others rare. The frequent types are seven in number, and in each of them a different chromosome must be doubled. Of the rarer ones each must also have one chromosome doubled, but in these cases other factors of the same rod must have been activated.

7. Among all the mutants, the new form *O. pulla* shows the least deviation from the original form *O. Lamarckiana*. It is therefore assumed to have its factors located in the central chromosome. The remaining six types are those of the old dimorphic races, each of them designating a lateral chromosome, as had already been deduced by us from other considerations. The rarer types are such as have previously been pointed out as secondary ones. It is assumed that *oblonga* and *auricula* have their factors in the *scintillans* chromosome, whereas *candicans* is derived from *cana* and *hamata* probably from *spathulata*.

8. In order to get sufficiently sharply distinguished types among the progeny of *semigigas*, some conditions must be fulfilled. In the first place, *velutina* pollen should be used for the fertilization, since its qualities, as a rule, are recessive to those of the mutants. Then the culture must be made under favorable conditions, as in the glass covered part of the garden. Also, the young seedlings should be planted singly in small pots, and selected and arranged shortly before being transplanted on the beds. If this is done the mutants belonging to the same type will flower next to one another, thereby giving a striking survey of the uniformity of their main features.

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NEW AMERICAN MEIBOMIAS

S. F. Blake

(WITH PLATE IV)

The late Joseph H. Painter of the United States National Herbarium undertook a monograph of the American species of *Meibomia* (*Desmodium*) a number of years ago, but never carried it far. At intervals during several years the writer has been occupied in the attempt to carry out a revision of this genus, but the pressure of other work has compelled the abandonment of the plan. A number of species described by the older investigators, and not recognized in recent years, have been found in the material examined, and it has been possible to reduce a number of names to certain or probable synonymy. So many of the earlier species are inadequately described, however, that an examination of several European herbaria is necessary to settle their identity, and a thorough revision of the genus is not practicable at the present time. The present paper, therefore, is limited to the description of a dozen new species from Mexico and Central and South America, and the discussion of a few other forms.

In addition to the large amount of material in the National Herbarium, I have examined, through the kindness of Dr. N. L. Britton and Dr. B. L. Robinson, several sheets from the New York Botanical Garden, and a large number from the Gray Herbarium, which have been of great assistance in the prosecution of the work. In the following descriptions, the measurements of the calyx lips are taken from the base of the calyx; those of the loment include the stipe when present. Unless otherwise cited, all specimens listed are in the United States National Herbarium.

Meibomia pycnantha, sp. nov.—Shrub, 1.6–5 m. high, branching; stem appressed-pilose, glabrescent, leafy; stipules medium-sized, deciduous; leaflets 3, elliptic, large, accumbent-pilose and at first sericeous beneath; racemes axillary and terminal, short, very densely flowered, spikelike, comose; bracts suborbicular-ovate, rather abruptly short-acuminate; flowers medium, short-pedicelled;

calyx silky-pilose; loment of *Heteroloma* type, stipitate, straight or curved, flat, pilosulous, the joints 2–4, obliquely oval or ovate-oval, about 7 mm. long. Fig. 2.

Stem rather stout, purplish brown, at first densely appressed- or ascending-pilose; stipules lanceolate, 6 mm. long, acuminate brown, appressed-pubescent; stipels narrowly subulate, quickly deciduous, 3 mm. long; petiole (1.2–4 cm. long) and rachis (8–22 mm.) appressed- or ascending-pilose; petiolules 2–4 mm. long; leaflets elliptic or narrowly ovate-elliptic, obtuse, mucronulate, rounded at base, papery, above dull green, evenly accumbent-pilose (hairs with slightly enlarged bases), beneath paler, at first densely silky-pilose, at maturity evenly accumbent-pilose, densely so along costa, prominulous-reticulate beneath in age (lateral veins about 8 pairs), terminal one 3.5–9.5 cm. long, 1.5–3 cm. wide, lateral about one-quarter smaller; racemes at first conical, densely bracteate, in bud and anthesis 1.5–2.5 cm. long, at maturity 5.5 cm. long or less, short peduncle (about 5 mm. long) and axis densely silky-pilose; bracts deciduous after anthesis, firm, purplish-tinged, striatulate, pilose-ciliate and appressed-pilose toward base with white hairs, body suborbicular-ovate, 3–4 mm. long, acumination 1–2.5 mm. long; pedicels paired, pilose, 3–4 mm. long, decurved in fruit; calyx 4 mm. long, lobes all subequal, upper lip entire, obtuse, lobes of lower lip triangular, acute; corolla with some purple, pale when dried, banner 1 cm. long; stipe of loment 3–4.5 mm. long, exceeding the withered calyx; loment 1.8–3.5 cm. long, shallowly or rather deeply lobed on upper margin, much more deeply so on lower, isthmi short or sometimes 1 mm. long; joints whitish, reticulate, evenly but sparsely curved-pilosulous on surface, more densely so on margin and there sometimes finely uncinate-hispidulous, 6–9 mm. long, 4–6 mm. wide.

MORELOS.—Mountain side above Cuernavaca, altitude 2440 m., February 2, 1899, *Pringle* 8046 (type no. 1,166,602, U.S. Nat. Herb.).

STATE OF MEXICO.—Dry hills, Salto de Agua, November, 1905, *Purpus* 1744.

This fine species is a member of the *Meibomia amplifolia* group, allied to *M. densiflora* (Hemsl.) Kuntze and *M. conzattii* (Greenm.) Standl. It is easily distinguished from *M. conzattii* by its densely pilose ovary (in *M. conzattii* merely pilosulous) and the much shorter acuminations of the bracts, these being 3–6 mm. long in *M. conzattii*. No material agreeing with HEMSLEY's descrip-

tion of *Desmodium densiflorum* has been examined, but his description applies so well in nearly all details to *M. conzattii* as to lead to the suspicion that the two are identical. The chief discrepancies are in the flowers, which are described as sessile by HEMSLEY, and the ovary, which is described as glabrous. The type collection of *M. pycnantha* was distributed without name, and PURPUS' plant as "*Desmodium? densiflorum.*"

Meibomia sylvestris, sp. nov.—Herbaceous or suffrutescent, branching; stem finely uncinate-puberulous and often sparsely hirsute, glabrate or glabrescent; stipules deciduous; leaves slender-petioled; leaflets 3, ovate, antrorse-pilose on both sides, sometimes glabrate above; racemes usually panicled, elongate, loose; bracts small, deciduous; pedicels 1–2 cm. long, flowers medium; loment of *Heteroloma* type, subsessile or stipitate, the 3–6 joints usually half-rhombic, densely uncinate-hirsutulous, 7–10 mm. long. Fig. 1.

Stem rather slender, terete, up to 2 m. high, usually glabrate; stipules subulate-attenuate, about 6 mm. long; stipels bristleform, 2–4 mm. long; petiole (2–4.5 cm. long) and rachis (6–17 mm.) hirsutulous or glabrate; leaflets ovate, varying to elliptic-ovate or broadly ovate, obtuse, mucronulate, rounded at base, thin, sometimes becoming pergamentaceous in age, above deep green, evenly but not densely antrorse-pilose (hairs with small tuberculate bases), sometimes glabrate, beneath similarly pubescent, prominulous-reticulate beneath in age, terminal one 3.2–7.5 cm. long, 2–4 cm. wide, lateral usually about one-third smaller; racemes peduncled, up to 25 cm. long, axis densely uncinate-hispidulous and sparsely hirsute; pedicels usually paired, uncinate-puberulous, spreading or ascending in fruit; bracts lance-subulate, 4.5 mm. long, striate, flavescent-hirsute; calyx flavescent-hirsute and minutely puberulous, upper lip bidenticulate, 4.8 mm. long, lower 5.8 mm. long; corolla "violet," banner 11 mm. long; stipe of loment usually 2–5 mm. long and equaling or exceeding the withered calyx, sometimes obsolete; loment straight, shallowly lobed on upper margin, deeply so on lower, 2.8–6.2 cm. long; joints half-rhombic or sometimes nearly oval, golden brown in age, 6–10 (rarely 14) mm. long, 5–6 mm. wide.

COLOMBIA.—In forest, Cordillera Oriental, east of Neiva, Dept. Huila, altitude 1800–2300 m., August 1–8, 1917, *Rusby & Pennell* 577 (type in herbarium of N.Y. Bot. Gard.; fragment in U.S. Nat. Herb.); forest slope,

Tequendama, Dept. Cundinamarca, altitude 2200–2300 m., September 15, 1917, *Pennell* 1980; in forest above Fusagasuga, Dept. Cundinamarca, altitude 1800–2300 m., November 28–29, 1917, *Pennell* 2690; edge of forest above Saliento, Dept. Caldas, altitude 2100–2500 m., July 25–31, 1922, *Pennell* 8885.

Related to *Meibomia orizabana* (Hemsl.) Kuntze, which has a nearly or quite simple, usually strongly angled and essentially glabrous stem, acuminate and nearly or quite glabrous leaflets, and a non-hirsute calyx. *Meibomia orizabana*, originally described from the region of Orizaba, Veracruz, occurs also in Oaxaca (*Conzatti* 3819), Chiapas (*E. W. Nelson* 3257), Costa Rica (*Pittier* 16614, *Tonduz* 12628), and Colombia (Popayan, *Lehmann* [no. 5114 in N.Y. Bot. Gard.; no. B. T. 376, in Gray Herb.]; Dept. El Cauca, *Pennell & Killip* 8049; Dept. Caldas, *Pennell* 10661, 10729; Dept. Antioquia, *Pennell* 10791). The detailed description of *Hedysarum caripense* H.B.K. (=*Meibomia caripensis* [H.B.K.] Kuntze), from Caripe, Cumaná, agrees so well with *M. orizabana* as to render it almost certain that the two species are identical.

One of PENNELL'S specimens of *M. orizabana* (no. 10729) shows a regularly pinnate 5-foliolate leaf, in addition to normal 3-foliolate leaves, and another leaf of the same specimen is 4-foliolate, the extra leaflet in this case being much smaller than the other three, and borne at the apex of the rachis beside the terminal leaflet. I have seen no other specimens of *Meibomia* with more than 3 leaflets, but BENTHAM states in the *Genera Plantarum* that the leaves are very rarely 5-foliolate, and HARMS (Repert. Sp. Nov. Fedde **10**:132. 1911) mentions several species with 5-foliolate leaves from New Guinea and New Caledonia.

Meibomia tephrophylla, sp. nov.—Shrub; stem uncinate-hispidulous and hirsute-pilose; stipules lance-subulate, 4 mm. long, subpersistent; leaflets 3, usually linear-oblong, obtuse to broadly rounded, sparsely antrorse-pilose above, more densely so beneath, grayish green; racemes panicled, about 15 cm. long; bracts small; pedicels about 5 mm. long; loment of *Heteroloma* type, stipitate, straight, cinereous-pilosulous with straight hairs, the 2–3 joints obliquely obovate or semiorbicular, often obscurely indented above, about 10 mm. long, 6 mm. wide. Fig. 6.

Stem slender, terete, apparently simple below inflorescence, densely uncinate-hispidulous with spreading hairs and less densely hirsute-pilose with straight, spreading, ascending, or sometimes subappressed hairs; stipules dry, ciliate, persistent or deciduous; stipels very narrow, persistent, 1–2 mm. long; petiole (6–10 mm. long) and rachis (4–8 mm.) deeply grooved above, pubescent like the stem; petiolules 1–2 mm. long; leaflets linear-oblong, elliptic-oblong, or lower sometimes lance-ovate or oval-ovate, apiculate,

rounded or subcordate at base, firm, lateral veins (4–7 pairs) scarcely prominulous above, prominent beneath, secondaries loosely prominulous-reticulate beneath, terminal leaflet 3.5–5.8 cm. long, 8–14 mm. wide, lateral about half as large; racemes several, subsessile, rather loosely flowered, axis and pedicels densely uncinate-hispidulous; bracts deciduous, not well seen; pedicels in clusters of 1–4, 3.5–5 mm. long, spreading in fruit; calyx hirsute-pilose and hispidulous with straight hairs, upper lip bidentate, 3 mm. long, lower lip 3.5 mm. long, its lobes acuminate, middle one longest; corolla purple, 7.5 mm. long; stipe of loment 4–5 mm. long, greatly surpassing the withered calyx; loment 2.2–3 cm. long, rather densely cinereous-pilosulous, especially on margin, shallowly lobed above, deeply so below, joints 9–12 mm. long, 5–6.5 mm. wide.

JALISCO.—Barranca of Guadalajara, May 1, 1894, *Pringle* 5880 (type no. 316751, U.S. Nat. Herb.).

The material examined consists of a portion of leafy stem and two defoliate portions of stem bearing flowers and fruit. The species is evidently one of the *M. cajanifolia* group, nearest *M. cinerea* (H.B.K.) Standl., which has much broader and more pubescent leaflets and much smaller joints.

Meibomia ciliaris (Muhl.) Blake.—*Hedysarum ciliare* Muhl.; Willd. Sp. Pl. **3**:1196. 1803; *Desmodium ciliare* DC. Prodr. **2**:329. 1825.

In our manuals this species is given a range from Massachusetts to Florida, west to Ontario, Michigan, Missouri, and Texas. It occurs also in Cuba[1] (*Wright* 2318, from Pinales, Caimito,[2] September 13; Gray Herb.) and Haiti.[3] Hitherto it has not been recorded from Mexico, and its occurrence so far south as Oaxaca, without intermediate stations, is very surprising. There is a sheet in the National Herbarium (no. 1,166,601), bearing three specimens in flower and fruit, collected by E. W. NELSON (no. 2694) near Santo Domingo, Oaxaca, altitude 485 m., June 18, 1895, which the most careful comparison has failed to distinguish in any character from *M. ciliaris*. It is true that all the stems terminate in simple racemes, while every specimen of *M. ciliaris* examined from other localities is more or less branched; but this is not likely to be more than an individual variation, and is covered by current descriptions of *M. ciliaris*. The possibility of error in the association of label and specimens

[1] GRISEBACH, Cat. Pl. Cub. 73. 1866.

[2] From the dates and other information given in UNDERWOOD's paper on WRIGHT's explorations in Cuba, Bull. Torr. Bot. Club **32**:291–300. 1905, it is evident that this locality is in either Matanzas or Habana.

[3] URBAN, Symb. Antill. **8**:293. 1920. Specimens collected near Furcy by LEONARD (no. 4750) are in the National Herbarium.

is obviated by the fact that to one of the stems is still tied the original collecting tag, bearing the number corresponding to the label.

For thirty years American investigators, following VAIL,[4] have united *Hedysarum obtusum* Muhl. and *H. ciliare* Muhl. under the name *Meibomia obtusa* or *Desmodium obtusum*, the two names of MUHLENBERG being considered synonymous, and *H. obtusum* having page priority. TORREY and GRAY[5] were in some doubt as to the proper reference for the type of *H. obtusum* in the WILLDENOW herbarium, but considered that it was probably a smoother variety of *D. ciliare*, rather than a form of *D. marilandicum*. URBAN[6], however, has recently used the name *Desmodium ciliare*, remarking that the types of *H. ciliare* and *H. obtusum* in the WILLDENOW herbarium appear to be very different plants. Under these circumstances it seems best to readopt the name *ciliare*, the description of which is unequivocal. *H. obtusum* will probably prove to be a form of *M. marilandica*, as the description suggests, and as the earlier investigators interpreted it.

Meibomia cana (Gmel.) Blake.—*Hedysarum racemosum* Aubl. Pl. Guian. **2**:774. 1775; *H. supinum* Swartz, Prodr. Veg. Ind. Occ. 106. 1788 (not *Hedisarum supinum* Chaix; Villars, Prosp. 41. 1779–80); *H. incanum* Swartz, Prodr. Veg. Ind. Occ. 107. 1788 (not *H. incanum* Thunb. Fl. Jap. 289. 1784); *H. canum* Gmel. Syst. Veg. **2**²:1124. 1791; *H. racemiferum* Gmel. Syst. Veg. **2**²:1125. 1791; *?Desmodium racemiferum* DC. Prodr. **2**:331. 1825; *D. incanum* (Swartz) DC. Prodr. **2**:332. 1825; *D. supinum* (Swartz) DC. Prodr. **2**:332. 1825; *Meibomia adscendens β. incana* (Swartz) Kuntze, Rev. Gen. Pl. **1**:195. 1891; *M. racemifera* (DC.) Kuntze, Rev. Gen. Pl. **1**:198. 1891; *M. supina* (Swartz) Britton, Ann. N.Y. Acad. Sci. **7**:83. 1892; *Desmodium canum* (Gmel.) Schinz & Thellung, Mém. Soc. Neuchât. Sci. Nat. **5**:371. 1914.

The principal synonyms of this much-named species are given in this list. *Hedysarum racemosum* Aubl., *H. canum* Gmel., and *H. racemiferum* Gmel. are all based primarily on a figure in BURMANN'S edition[7] of PLUMIER. This figure represents the plant usually known as *Desmodium incanum*, *D. supinum* or *Meibomia supina*, the acute-elliptic or oval-elliptic leaflets and the persistent bracts of the raceme being definitely those of *M. supina* and not of *M. adscendens* (Swartz) Kuntze. The earliest name, *Hedysarum racemosum* Aubl., is not available, being preoccupied under *Meibomia* and *Desmodium* by *M. racemosa* (Thunb.) Kuntze and *D. racemosum* (Thunb.) DC., both based on *H. racemosum* Thunb. (1784). *Hedysarum supinum* Swartz is preoccupied by *Hedisarum*

[4] Bull. Torr. Bot. Club **19**:115. 1892.

[5] Fl. N. Amer. **1**:362. 1840.

[6] Symb. Antill. **8**:292. 1920.

[7] PLUMIER, Pl. Amer. ed. BURMANN 140. *pl. 149. fig. 1.* 1757.

supinum Chaix ex Villars,[8] and *H. incanum* Swartz by *H. incanum* Thunb. The first available name, *Hedysarum canum* Gmel., must be taken up for the species.

The description of *Hedysarum guianense* Aubl. somewhat suggests this species, but the type in the British Museum is *M. barbata* (L.) Kuntze, as I have been informed by Mr. E. G. BAKER.

Meibomia acuminata (Michx.) Blake.—*Hedysarum acuminatum* Michx. Fl. Bor. Amer. **2**:72. 1803; *H. glutinosum* Muhl.; Willd. Sp. Pl. **3**:1198. 1803; *Desmodium acuminatum* DC. Prodr. **2**:329. 1825; *Desmodium grandiflorum* and *Meibomia grandiflora* Amer. auth. (not *Hedysarum grandiflorum* Walt. 1788).

This very distinct species was almost universally known as *Desmodium acuminatum* until 1891, when OTTO KUNTZE adopted for it, without discussion, the name *Meibomia grandiflora* (Walt.) Kuntze,[9] based on *Hedysarum grandiflorum* Walt.[10] WALTER'S plant, which is not mentioned by MICHAUX, PURSH, ELLIOT, TORREY and GRAY, or any other of the earlier writers on North American plants, and which was listed by DECANDOLLE among the "species trifoliate non satis notae" as *Desmodium grandiflorum*, was apparently first noticed again by SERENO WATSON, who cited it (Bibl. Ind. N. Amer. Bot. 215. 1878) as a synonym of *Desmodium acuminatum*. It was probably on the basis of this reference that KUNTZE was led to adopt the name in this sense.

Aside from the fact that the name *grandiflorum* is preoccupied in *Hedysarum* by *H. grandiflorum* Pall. (Reise **2**:743. 1773), and so is not available under the American Rules, it is clear from WALTER'S description, quoted below that he could not have referred to the plant under consideration. The species now passing as *Desmodium grandiflorum* or *Meibomia grandiflora* has the leaves crowded at the summit of a stem about a foot long, which bears at its apex a single, naked, long-peduncled raceme or panicle; the leaflets are not noticeably veiny, the loments are 2- or 3-jointed, and the flowers are not notably large. WALTER'S description, however, calls for a plant with veiny leaves, axillary racemes, many-jointed loments, and large flowers. WALTER'S fragmentary type is still preserved in his herbarium at the British Museum, where it has been examined for me and compared with authentic material by Mr. E. G. BAKER. Mr. BAKER reports that the type has leaflets glabrous beneath, conspicuous and persistent stipels, ovate, acuminate, strongly striate bracts, and uncinate-

[8] Mr. T. F. CHIPP, Assistant Director of the Royal Botanical Gardens at Kew, has kindly forwarded a copy of VILLARS' description, taken from the copy of his work in the library of the Linnean Society. VILLARS' work is very rare and apparently is not in any American library.

[9] Rev. Gen. Pl. **1**:196. 1891.

[10] WALTER, Fl. Carol. 185. 1788: "*grandiflorum* 6. fol. ternatis ovalibus *venosis utrique laevibus;* racemis axillaribus erectis, leguminibus pendulis multiarticulatis, floribus majoribus."

hirsutulous inflorescence. The specimen shows no stipules, and is too small to show whether the leaves are scattered along the stem.

In all the positive characters mentioned, WALTER's type disagrees with the plant now passing as *Meibomia grandiflora* or *Desmodium grandiflorum*, but does agree with *M. bracteosa*. WALTER's description, moreover, applies well to this species, which has the largest flowers of any eastern species except *M. canadensis*. Several specimens of these two species (*M. bracteosa* and *M. "grandiflora"*) were sent to Mr. BAKER, who states that a specimen of *M. bracteosa* (*Standley* 9809) agrees best with WALTER's type.

From the information supplied by Mr. BAKER, as well as from WALTER's own description, it is clear that the names *Meibomia grandiflora* (Walt.) Kuntze and *Desmodium grandiflorum* (Walt.) DC. must now be transferred to the plant at present called *Meibomia bracteosa* (Michx.) Kuntze or *Desmodium bracteosum* (Michx.) DC, and that MICHAUX's name *acuminatum* must be adopted once more for the plant to which WALTER's name has been misapplied for a generation.

Meibomia rhynchodesma, sp. nov.—Suffrutescent(?), scandent; stem uncinate-hirsutulous; leaves slender-petioled; leaflets 3, ovate, large, glabrate above, rather densely whitish-pilosulous beneath; panicles large, loose; flowers small; loment of *Nephromeria* type, stipitate, rufid-pilosulous on margin, somewhat puberulent on surface; joints 1–2, suborbicular, about 1.8 cm. long, strongly inflexed and beaked at apex, upper margin notched, its length half to two-thirds that of the middle of the body. Fig. 3.

Stem slender, subterete, flexuous, flavescent-hirsutulous with mostly ascending uncinate hairs and minutely puberulent, glabrescent; stipules and stipels deciduous, not seen; petiole (2.5–4.5 cm. long) and rachis (about 1.8 cm.) sparsely uncinate-hispidulous; petiolules 2–3 mm. long; leaflets ovate or broadly ovate, acute or obtusish, rounded at base, papery, above dull green, beneath paler and prominulous-reticulate (lateral veins 4–5 pairs), terminal one about 8 cm. long, 5–6.2 cm. wide, lateral 5.5–7 cm. long, 3–4 cm. wide; panicles axillary, uncinate-hirsutulous, branches widespreading; bracts deciduous, not seen; pedicels solitary or paired, uncinate-puberulous, 3–7 mm. long; calyx short-ciliate, sparsely hirsute on lowest lobe, upper lip bidentate, 3 mm. long, lower lip 4 mm. long, lobes ovate or oblong-ovate, apiculate, middle one longest; corollas about 6 mm. long, not well seen; stipe of loment 3–5 mm. long, much exceeding the withered calyx; loment 1.3–2.5 cm. long on upper margin, shallowly lobed on upper margin, very

deeply on lower; joints (submature) 1–1.2 cm. long on upper margin, 1.3–1.9 cm. long across middle of body, 1.6–1.9 cm. wide, densely rufid-pilosulous on margin, on body puberulous and sparsely pilose, reticulate, upper margin with a notch 1–2 mm. deep, seed borne somewhat above the center.

COSTA RICA.—In thickets, Tuis, altitude 650 m., November 1897, *Tonduz* 11448 (type no. 694364, U.S. Nat. Herb.).

A member of the *Nephromeria* group, related to *M. macrodesma* Blake and *M. purpusii* (T. S. Brandeg.) Blake. Both *M. macrodesma* and *M. rhynchodesma* differ from *M. purpusii* in having the upper margin of the joints of the loment only half to two-thirds as long as the central portion of the body. From *M. macrodesma*, *M. rhynchodesma* is distinguished by the dull white (not rufid) pubescence of the leaves and the smaller, merely puberulous loment joints, which at apex are prominently inflexed and beaked.

Meibomia crotalum, sp. nov.—"Climbing herb"; stem uncinate-hirsute; stipules mostly deciduous; leaflets 3, ovate, obtuse, large, persistently puberulous above, densely and softly pilose beneath; racemes panicled; flowers rather small; loment of *Nephromeria* type, short-stiped or subsessile; joints 1–2, reniform-suborbicular, ciliolate, about 2–2.5 cm. long, slightly beaked, upper margin notched, its length two-thirds to three-fourths that of the middle of the body. Fig. 4.

Stem slender, branched, densely uncinate-hirsute with rufescent hairs and sometimes densely and finely pilosulous, at length glabrate; stipules triangular-ovate, striate, hirsute-ciliate, about 7 mm. long, erect, at length brown and deciduous; stipels about 3 mm. long, often deciduous; petiole (2.5–4 cm. long) and rachis (8–16 mm.) densely hirsute-pilose with straight or hooked reddish brown hairs; petiolules 2–3 mm. long; leaflets ovate or broadly ovate, obtuse or rounded, mucronulate, broadly rounded to subcordate at base, papery, above dull green, beneath densely antrorse-pilose with grayish hairs, along the chief veins rufescent-pilose, feather-veined (chief veins 4–7 pairs) and in age definitely prominulous-reticulate beneath, terminal one 4.5–9 cm. long, 2.5–6 cm. wide, lateral about one-quarter smaller; racemes loose, axillary and terminal, up to about 20 cm. long, pubescent like the stem; bracts ovate, 4–5 mm. long, acuminate, striate, hirsute, deciduous; pedicels paired, spreading in fruit, uncinate-hirsutulous, 6–9 mm. long; calyx thin, hirsute and hirsutulous, upper lip 3.5 mm. long, acutely bidentate, lower

4 mm. long, the 3 lobes acuminate, middle one much the longest; corolla "violet-blue" or "purple-violet," banner 6 mm. long; stipe of loment 1–3 mm. long, about equaling the withered calyx, usually stout; pod straight, 1.5–3.8 cm. long on upper margin, slightly lobed on upper margin, very deeply so on lower, isthmus marginal, 1.5–3 mm. wide, joints broadly overlapping; joints greenish-white, reticulate, rufid-ciliolate especially on lower margin, glabrous on sides or obscurely puberulous in region of seed, usually very slightly beaked at apex, deeply notched on upper margin, 1.3–2 cm. long on upper margin, 2–2.8 cm. long across middle of body, 1.9–2.5 cm. wide.

COLOMBIA.—In thickets, Cuchilla, east of Zarzal, Dept. El Valle, Cauca Valley, altitude 1100–1400 m., July 22, 1922, *F. W. Pennell, E. P. Killip, & T. E. Hazen* 8531 (type no. 1,143,492, U.S. Nat. Herb.); along stream, La Cumbre, Dept. El Valle, Cordillera Occidental, altitude 1500–1600 m., May 21–25, 1922, *Pennell & Killip* 5976; in forest, Tabeja, west of Armenia, Dept. Caldas, Cauca Valley, altitude 1100–1300 m., July 23, 1922, *Pennell, Killip, & Hazen* 8631; open land near Rio San Joaquin, La Gallera, Micay Valley, Dept. El Cauca, Cordillera Occidental, altitude 1400–1500 m., June 29–30, 1922, *Killip* 7854.

Allied to *M. metallica* Rose & Standl., *M. albonitens* (Lem.) Rose & Standl., *M. purpusii* (T. S. Brandeg.) Blake, *M. macrodesma* Blake, and *M. rhynchodesma* Blake; distinguished by its short-stiped loment, which is nearly or quite glabrous except on margin, and its blunt leaflets, which are densely puberulous above and densely soft-pubescent beneath. *Meibomia crotalum* is the first species of its immediate group to be found in South America.

Meibomia infracta (DC.) Blake.—*Desmodium infractum* DC. Prodr. **2**:330. 1825; Moc. & Sessé, Calques des Dessins *pl. 270; Hedysarum biarticulatum* Moc. & Sessé; DC. Prodr. **2**:330. 1825, as synonym (not *H. biarticulatum* L. 1753); *Desmodium barclayi* Benth. Bot. Voy. Sulph. 83. 1844; *Meibomia barclayi* Rose & Standl. Contr. U.S. Nat. Herb. **16**:216. *pl. 51, fig. e.* 1913.

An earlier name for *Desmodium barclayi* Benth. is found in *D. infractum* DC., based on plate 270 of the Calques des Dessins of MOCIÑO & SESSÉ, drawn from a plant from "Mexici montibus." BENTHAM, when describing *D. barclayi*, recognized its relationship to *D. infractum*, but inferred a difference in the shape of the loment joints. Examination of the reproduction of MOCIÑO & SESSÉ's plate, in connection with DECANDOLLE's description, leaves no doubt of the identity of the plants concerned. HEMSLEY (Biol. Centr. Amer. Bot. **1**:275. 1880) recorded *D. barclayi* from Guatemala, Nicaragua, Panama, and Venezuela. In their revision of the *Nephromeria* group, ROSE and STANDLEY

were able to cite material only from Costa Rica. The following specimens, all in the National Herbarium unless otherwise noted, have been examined by the writer:

VERACRUZ.—Puente Nacional, *Purpus* 6089 (fl.).

MICHOACÁN or GUERRERO.—La Correa, *Langlassé* 418 (fl.); La Botella, *Langlassé* 658 (fr.; Gray Herb.; ident. by MICHELI as *D. scutatum*).

OAXACA.—Guatulco, *Liebmann* (fr.); Cafetal Concordia, *Reko* 3362 (fl., fr.); District of Tuxtepec, *Conzatti* 3757 (fr.).

HONDURAS.—Isla Tigre, *Standley* 20735 (fr.).

SALVADOR.—Vicinity of Ahuachapán, *Standley* 19815 (fr.).

COSTA RICA.—Nicoya, *Tonduz* 13577 (fr.).

COLOMBIA.—Vicinity of Cartagena, 1919, *Bro. Heriberto* 245 (fl., fr.).

VENEZUELA.—Colonia Tovar, *Fendler* 1790 (fr.; Gray Herb.).

ECUADOR.—Guayaquil, 1923, *H. E. Anthony* 76 (fr.).

Meibomia psilacra, sp. nov.—Herbaceous, branched; stem densely uncinate-hirsutulous, inflorescence short-pilose with glandular-based hairs; stipules mostly persistent, lance-ovate, about 6 mm. long; leaflets 3, ovate, hirsute and hirsutulous especially toward margin and uncinate-hispidulous; racemes axillary and terminal, loose, elongate; bracts small, deciduous; pedicels spreading or ascending, 1–1.5 cm. long; flowers small; loment of *Chalarium* type, short-stipitate or subsessile, the 1–5 joints oval, about 9 mm. long, terminal one hispidulous on margin, otherwise essentially glabrous, others uncinate-hispidulous on margin and surface. Fig. 7.

Perennial, 30–60 cm. high; stem slender, subterete, green or purplish, densely uncinate-hirsutulous with ascending to deflexed hairs and finely puberulent; stipules stiff, acuminate, striate, purplish, erect or reflexed in age; stipels bristleform, about 1.5 mm. long; petiole (7–17 mm. long) and rachis (4–8 mm.) pubescent like the stem; petiolules 1–2 mm. long; leaflets obtuse or acute, mucronulate, rounded at base, pale green, firm-papery, above sparsely hirsute and somewhat uncinate-hirsutulous, toward margin densely hirsutulous with straight hairs, beneath similarly pubescent and prominulous-reticulate (lateral veins about 5 pairs), terminal one 1.8–3.8 cm. long, 1–2.2 cm. wide, lateral usually about half as large; racemes peduncled, panicled above, 10–30 cm. long, axis and pedicels short-pilose with spreading hairs with glandular yellowish bases, and finely puberulous; bracts subulate-ovate, 3 mm. long, acuminate, hirsute and puberulous, greenish; pedicels solitary or paired; calyx hirsute and puberulous, upper lip bidentate, 3.2 mm. long,

lower 4.5 mm. long, lateral lobes oblong, obtuse, middle one longer, triangular-ovate, acute; corolla purplish, about 8 mm. long; stipe of loment 1–2 mm. long, equaling or surpassing the withered calyx; loment equally lobed on both margins or slightly more deeply lobed beneath, straight or curved, flat or often somewhat twisted, 1.2–3.5 cm. long; joints usually 3 or 4, rarely 1 or 5, thin-walled, prominulous-reticulate, sometimes indented on upper margin, often (especially proximal joints) with somewhat inflexed margins, 8–10.5 mm. long, 6–7 mm. wide, all but terminal one rather sparsely uncinate-hispidulous on surface, densely so on margin, terminal one hispidulous with mostly straight hairs on margin, its body shining and nearly or quite glabrous.

SINALOA.—Sandy soil along river, near Fuerte, March 25, 1910, *J. N. Rose, P. C. Standley, & P. G. Russell* 13475 (type no. 636300, U.S. Nat. Herb.); dry hillside west of Álamos, March 16, 1910, *Rose, Standley, & Russell* 12960.

Allied to *Meibomia psilocarpa* (A. Gray) Kuntze, in which the loment is glabrous throughout except for some uncinate hairs on the margin.

Meibomia bella, sp. nov.—Shrubby, tall; stem strigose and finely pulverulent, inflorescence uncinate-hispidulous; stipules subulate-attenuate, reflexed, deciduous; leaves slender-petioled; leaflets 3, elliptic-ovate or ovate, prominulous-reticulate, firm, sparsely pubescent or glabrous above, sparsely strigose or antrorse-pilose on veins beneath; racemes numerous, panicled, comose at apex; bracts ovate, acuminate, 6–8 mm. long; pedicels about 1 cm. long; flowers large; loment of *Chalarium* type, stipitate, straight or usually somewhat twisted, sparsely crisped-puberulous, the 3–8 joints obliquely oval, about 3.5 mm. long. Fig. 10.

Branching, 2–3.3 m. high; stem slender, terete, usually purplish, densely pulverulent and less densely strigose, without hooked hairs below the inflorescence; stipules brownish, 4–7 mm. long; stipels bristleform, 2–3.5 mm. long, sometimes deciduous; petiole (2–5.5 cm. long) and rachis (5–13 mm.) strigose; leaflets obtuse or acute, mucronulate, rounded at base, above green, sometimes with lighter stripe along costa, sparsely strigose or strigillose or sometimes glabrous, beneath paler green, strigose or antrorse-pilose along costa and usually along chief veins, terminal one 2.5–5.5 cm. long, 0.8–2.3 cm. wide, lateral about one-third smaller; racemes several or numerous, terminal and axillary, loose below, up to 30 cm. long,

terminal one compound, axillary ones often simple; bracts purplish, hirsute-ciliate, deciduous; pedicels mostly paired, uncinate-hispidulous, erectish or somewhat spreading in fruit, 6–12 mm. long; calyx long-hirsute on lowest lobe, sparsely pubescent elsewhere, upper lip bidenticulate, 4 mm. long, lower lip 6 mm. long, middle lobe much longer than lateral; corolla purple, the broad banner 13 mm. long; stipe of loment 3–5 mm. long, considerably surpassing calyx; loment 1.5–2.8 cm. long, essentially equally constricted on both margins, isthmi usually short, sometimes 1 mm. long, joints prominulous-reticulate, 3–3.8 mm. long.

MORELOS.—Mountain woods above Cuernavaca, altitude 2135 m., November 19, 1895, *Pringle* 6206 (type no. 254325, U. S. Nat. Herb.); Sierra de Tepoxtlan, altitude 2285 m., November 27, 1902, *Pringle* 9744.

MICHOACÁN.—At various localities near Morelia, altitude 1900–2800 m., 1909–1912, *Arsène* 3249, 5303, 5346, 5783, 7342, 8292, 10027.

Related to *Meibomia ghiesbreghtii* (Hemsl.) Kuntze and *M. subtilis* (Hemsl.) Kuntze, both of which are now represented in the National Herbarium by good suites of specimens. In *M. ghiesbreghtii* the loment and the lower surface of the leaves are entirely glabrous; in *M. subtilis* the pod is rather densely uncinate-puberulous; and in both species the long appressed hairs of the stem of *M. bella* are wanting. *Meibomia venusta* (Steud.) Kuntze (*Desmodium elegans* Schlecht., not DC.), also closely allied, and probably identical with *M. subtilis*, is described as showing on the stem "pilos uncinatos rectosque atque in faciebus minutissimos punctiformes," while in *M. bella* the stem is strigose and finely pulverulent, without uncinate hairs. PRINGLE'S no. 6206 was distributed as *D. uncinatum* DC., his no. 9744 as *D. elegans* Schlecht.

Meibomia subsessilis (Schlecht.) Blake.—*Desmodium subsessile* Schlecht. Linnaea **12**:319. 1838.

This species, apparently not recognized heretofore among recent collections, is represented by a number of specimens in the National Herbarium, of which the following may be cited:

HIDALGO.—*Pringle* 7913; *Rose* 7086, 8014.

PUEBLA.—*Purpus* 2682; *Arsène* 227, 1191, 1251, 1292, 5418, 5419, 7194, 10028.

OAXACA.—*L. C. Smith* 937; *Purpus* 3047; *Pringle* 4780; *Nelson* 1585.

It is related to *M. hartwegiana* (Hemsl.) Kuntze, and several of the specimens listed have been identified as that species. In *M. subsessilis* the leaflets are chiefly lance-ovate or ovate, tapering to the often obtuse apex, thickish, impressed-veined above, densely and softly cinereous-pilose beneath, while in *M. hartwegiana* they are chiefly elliptic, not tapering to apex, reticulate above but not impressed-veined, and less densely pubescent beneath. The following specimens in the National Herbarium agree with a flowering specimen in the

Gray Herbarium of *Hartweg* 56 from Aguas Calientes, type number of *Meibomia hartwegiana* (Hemsl.) Kuntze:

COAHUILA.—*Pringle* 13699.
DURANGO.—*Nelson* 4646, *Palmer* 663 (1896).
JALISCO.—*Rose* 2511, 3568.
HIDALGO.—*Pringle* 8245.
PUEBLA.—*Arsène* 480, 10026, 10030.

Meibomia leptomeres, sp. nov.—Perennial, erect, simple below the inflorescence; stem densely uncinate-hispidulous; stipules lance-subulate, dry, subpersistent, about 8 mm. long; leaves slender-petioled; leaflets 3, linear, conduplicate, sparsely pilose; racemes elongate, slightly comose at apex; bracts purplish, about 4.5 mm. long; pedicels about 2.5 mm. long, deflexed in fruit; flowers medium; loment of *Chalarium* type, subsessile, essentially glabrous, nearly or quite straight, joints 3–4, oval, about 3 mm. long. Fig. 9.

Stems few, about 90 cm. high, essentially herbaceous, slender, terete, purplish, leafy; stipules brownish, striate, reflexed or spreading, 6–10 mm. long, persistent or deciduous; stipels bristle-form, persistent, 3–5 mm. long; petiole (1.8–3 cm. long) and rachis (7–11 mm.) very slender, uncinate-hispidulous; petiolules 1–2 mm. long; leaflets usually conduplicate, obtuse, mucronulate, rounded at base, firm, dull green above, lighter green beneath, sparsely antrorse-pilose on both sides, prominulous-reticulate especially beneath (chief lateral veins about 12 pairs), terminal one 3.5–6.8 cm. long, 5–6 mm. wide (when unfolded), lateral 3–5.8 cm. long; racemes 4, axillary and terminal, simple or sometimes bifurcate, peduncled, up to 35 cm. long, loose at maturity, pubescent like the stem; bracts ovate, acuminate, striate, ciliolate, sparsely pubescent dorsally, deciduous; pedicels solitary or paired, uncinate-puberulous, 1.5–3 mm. long; calyx minutely puberulous and sparsely hirsute, upper lip bidentate, 4 mm. long, lower lip 4.2 mm. long, its lobes acutish, middle one slightly longer than lateral; corolla purple, banner 9 mm. long; loment 1–1.5 cm. long, equally lobed on both margins, glabrous or occasionally with a few short crisped hairs on isthmi and margin, isthmi strictly central, sometimes 1 mm. long, joints prominulous-reticulate, rather plump, 3–3.5 mm. long.

JALISCO.—In the Sierra Madre, west of Bolaños, September 15–17, 1897, *Rose* 2953 (type no. 301906, U.S. Nat. Herb.).

In habit and foliage this species much resembles *Meibomia arizonica* (S. Wats.) Vail, but in that plant the joints of the loment are uncinate-puberulous and much larger.

Meibomia tenuipes, sp. nov.—Suffrutescent?, much branched; stem densely spreading- or ascending-pilosulous with somewhat crisped, not hooked, whitish hairs; stipules triangular-ovate, reflexed, persistent, about 5 mm. long; leaflets 3, ovate, antrorse-pilose; racemes panicled, loose; bracts small, deciduous or subpersistent; pedicels 8–15 mm. long, spreading or ascending in fruit; flowers medium; loment of *Chalarium* type, long-stipitate, more or less twisted, finely puberulent on surface, on margin uncinate-hispidulous; joints 3–5, oval, about 4 mm. long, their margins irregularly inflexed. Fig. 8.

Plant 60 cm. high and more; stem slender, subterete or subangulate, leafy; internodes mostly 1.5–3.5 cm. long; stipules acuminate, fuscous; stipels narrow, 1.5–2 mm. long; petiole (1–4 cm. long) and rachis (6–14 mm.) pubescent like the stem; petiolules 1–3 mm. long; leaflets obtuse, mucronulate, rounded at base, submembranous, above deep green, slightly paler beneath, evenly and sometimes densely antrorse-pilose on both sides with whitish or (in old specimens) somewhat rufescent hairs, prominulous-reticulate beneath, terminal one 2–5.5 cm. long, 1.5–3.8 cm. wide, lateral about one-fifth smaller; racemes axillary and terminal, numerous, up to about 15 cm. long, axis spreading-pilose or -pilosulous and sometimes with some short uncinate hairs; bracts lance-subulate or lance-ovate, about 4 mm. long, sometimes irregularly persistent; pedicels solitary or paired, finely puberulent with mostly straight hairs; calyx puberulent, ciliolate, and sparsely pilose, upper lip bidentate, 3.5 mm. long, lower lip 4–5 mm. long, lateral lobes oblong, obtusish, middle one much longer, lance-ovate, acute; corolla purplish(?), banner 9 mm. long; stipe of loment 4–7 mm. long, greatly exceeding the withered calyx; loment nearly equally lobed on both margins, 1.7–2.8 cm. long, straight or curved; joints oval or rhombic-oval, prominulous-reticulate, greenish-white, 4–4.5 mm. long, 3–4 mm. wide.

GUATEMALA.—Between Jacaltenango and San Martín, altitude 1615–2135 m., December 24, 1895, *E. W. Nelson* 3604 (type no. 252311, U.S. Nat.

Herb.); Solalá, January 31, 1915, *E. W. D. Holway* 163; mountain sides, Antigua, altitude 1675 m., December 28, 1916, *Holway* 646.

This species apparently belongs in the group of *Meibomia intorta*,[11] where it is distinguished by its non-uncinate pubescence, long pedicels, and long-stipitate loments.

Meibomia cryptopoda, sp. nov.—Suffrutescent?; stem glabrous, sharply trigonous, with long internodes; stipules cordate-amplexicaul, persistent, longer than the petiole; leaflets 3, linear, more than 10 times as long as wide, revolute-margined, essentially glabrous; raceme terminal, slender, simple, elongate; flowers small; ovary replicate, puberulous.

Stem slender, 60 cm. high and more (base not seen), purple, obscurely granular, with few short branches; main internodes 4.5–9 cm. long; stipules lance-ovate, 8–12 mm. long, acuminate, becoming brownish, striate, erect or reflexed; stipels subulate, persistent, 2–3.5 mm. long; petiole (3–5 mm. long) and rachis (3–8 mm.) obscurely granular; leaflets obtuse, mucronulate, obtuse at base, firm, above dull green, minutely puberulous, glabrate, beneath paler green, glabrous, prominulous-reticulate especially beneath, terminal one 4–11 cm. long, 3–6 mm. wide, lateral about one-third smaller; raceme single, peduncled, about 11.5 cm. long, loosely flowered, slightly comose at apex, axis like pedicels uncinate-puberulous; bracts ovate, 4–5 mm. long, acuminate, striate, purplish-tinged, ciliolate, deciduous; pedicels solitary or paired, erect, 5–10 mm. long; calyx hispidulous, 5 mm. long, lips subequal, upper bidenticulate, lower 3-lobed, lobes oblong-ovate, obtusish, ciliolate, middle one slightly longest; corolla purplish, about 6 mm. long; ovary of *Chalarium* type, replicate, 3-jointed, puberulous with straight several-celled hairs, stipe 2 mm. long, equaling tube of calyx, isthmi central, joints oval, about 2 mm. long.

JALISCO.—Mountains near Talpa, altitude 1340–1525 m., March 7, 1897, *E. W. Nelson* 4027 (type no. 327057, U.S. Nat. Herb.).

As the ovary shows, this is a member of the group of species with replicate pods typified by *Meibomia plicata* (Schlecht. & Cham.) Kuntze. It is nearest *M. cordistipula* (Hemsl.) Kuntze, represented in the National Herbarium by

[11] **Meibomia intorta** (Mill.) Blake.—*Hedysarum intortum* Mill. Gardn. Dict. ed. 8, no. 11. 1768; *Desmodium uncinatum* (Jacq. 1798) DC.—See FAWCETT and RENDLE, Fl. Jam. 4:34, 1920, for synonymy.

Pringle 13421, from Tarascón, Michoacán, but differs in its very short-petioled leaves with linear, strongly revolute-margined, and much longer leaflets.

Meibomia urarioides, sp. nov.—Herbaceous?; stem sharply several-angled, glabrous; stipules small, persistent; leaves slender-petioled; leaflets 3, ovate, obtuse, sparsely strigillose on both sides, thin; racemes panicled; bracts small, deciduous; pedicels about 1.2 cm. long, wide-spreading in fruit; flowers small; loment of *Chalarium* type, stipitate, replicate, glabrous, the 3–5 joints suborbicular, about 3.5 mm. long. Fig.. 5.

Stem slender, 45 cm. long and more (base not seen), green, branching in inflorescence; internodes 3–13.5 cm. long; stipules subulate from a broad base, reflexed, brownish, 3 mm. long; stipels bristleform, 2 mm. long; petiole (2–3.5 cm. long) and rachis (5–8 mm.) slender, glabrous; petiolules about 1.5 mm. long; leaflets mucronulate, broadly rounded at base, nearly equally green on both sides, weakly prominulous-reticulate, terminal one 3–4.3 cm. long, 1.2–2.2 cm. wide, lateral about one-third smaller; racemes axillary and terminal, forming a loose panicle about 25 cm. long, the somewhat zigzag axes and pedicels hispidulous with spreading, curved, scarcely uncinate hairs; bracts ovate, acuminate, 2 mm. long; pedicels mostly paired, 1–1.5 cm. long; calyx hirsute, particularly on lowest lobe, upper lip bidentate, 2.8 mm. long, lower lip 3.2 mm. long, lobes ovate, acute or obtuse, lowest longest; corolla purplish, about 5 mm. long, not well seen; stipe of loment 2–3 mm. long, equaling or surpassing the withered calyx; loment 7–9 mm. long, equally constricted on both margins, closely replicate, isthmi short, central, joints thin-walled, greenish-white, prominulous-reticulate, glabrous or with a few minute hairs.

Jalisco.—Roadside between San Sebastian and Mount Bufa de Mascota, altitude 1370–2285 m., March 20, 1897, *E. W. Nelson* 4100 (type no. 327028, U.S. Nat. Herb.).

A member of the *Meibomia plicata* group, distinguished from its nearest ally, **Meibomia michelii** Blake (*Desmodium madrense* Micheli, Mém. Soc. Phys. Hist. Nat. Genève **34**:258. *pl. 10.* 1903; not *D. madrense* Hemsl. 1880) by its strongly angled stem, persistent stipules, longer petioles, and hirsute calyx.

Meibomia dasyacra, sp. nov.—Shrubby, branched; stem strigillose and near the nodes hispidulous, sometimes glabrate, inflores-

cence densely uncinate-hispidulous; stipules small, mostly deciduous; leaves short-petioled; leaflets 3, elliptic or oblong-elliptic, pilose-strigose above, beneath pale, evenly but not densely pilose and prominent-reticulate, at first softly flavescent-pilose on both sides; racemes panicled, elongate, scarcely comose, at apex flavescent-pilosulous; flowers small; ovary replicate, pubescent.

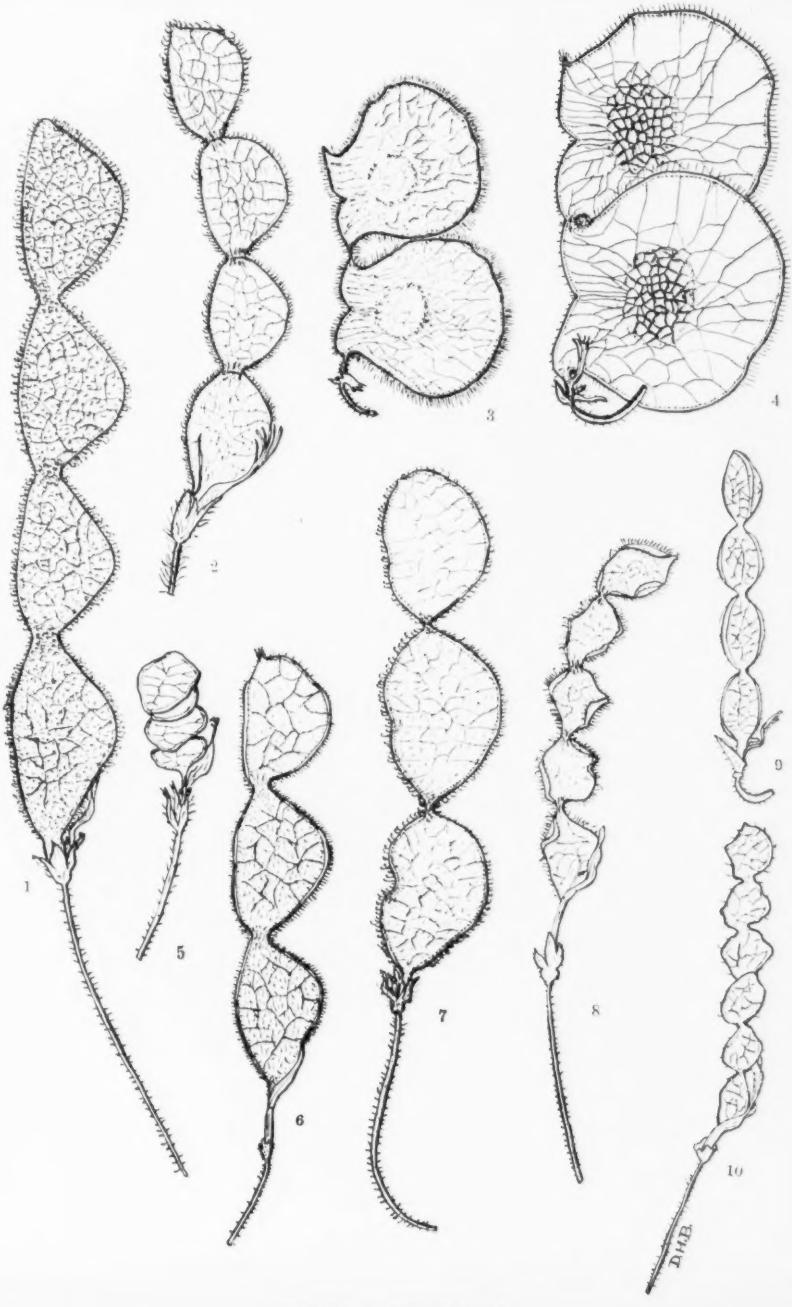
Stem slender, 45 cm. high and more, purplish; stipules subulate from a broad base, brown, firm, 3 mm. long, reflexed, rarely persistent; stipels bristleform, about 2 mm. long; petiole (0.5–1.5 cm. long) and rachis (2–10 mm.) ascending-hirsute, glabrescent; petiolules 1.5 mm. long; leaflets elliptic, elliptic-oblong, or rarely elliptic-ovate, obtuse, mucronulate, rounded at base, above light green, sparsely pilose-strigose, glabrescent, subulate in age, beneath curved-pilose on the raised whitish venation (lateral veins about 5 pairs), terminal one 4–7.5 cm. long, 1.5–2.5 cm. wide, lateral one-third to one-half smaller; racemes axillary and terminal, slender, rather loose in age, peduncled, 12 cm. long or less, axis and pedicels uncinate-hispidulous; bracts lanceolate, acuminate, densely flavescent-pilose, about 2.5 mm. long, deciduous; pedicels mostly in fascicles of 2–4, spreading, 3–5 mm. long; calyx densely flavescent-pilose, lips subequal, upper bidentate, 4–4.5 mm. long, lower 3-lobed, 4.5–5 mm. long, lobes ovate-lanceolate, acuminate, middle somewhat the longest; corollas purple, about 5 mm. long; ovary of *Chalarium* type, short-stiped, densely uncinate-hispidulous on margin, antrorse- or spreading-pilose on sides, joints 3–4, oval, about 3 mm. long.

JALISCO.—Mountains near Talpa, altitude 1340–1525 m., March 7, 1897, *E. W. Nelson* 4028 (type no. 327058, U.S. Nat. Herb.).

A member of the *Meibomia plicata* group, nearest *M. plectocarpa* (Hemsl.) Kuntze, which is readily distinguished by its oval or suborbicular leaflets, in addition to other characters.

EXPLANATION OF PLATE IV

Fruits of *Meibomia:* *1*, *Meibomia sylvestris* Blake (type), ×2; *2*, *M. pycnantha* Blake (type), ×2; *3*, *M. rhynchodesma* Blake (type), ×1; *4*, *M. crotalum* Blake (type), ×1; *5*, *M. urarioides* Blake (type), ×2; *6*, *M. tephrophylla* Blake (type), ×2; *7*, *M. psilacra* Blake (type), ×2; *8*, *M. tenuipes* Blake (*Holway* 163), ×2; *9*, *M. leptomeres* Blake (type), ×2; *10*, *M. bella* Blake (*Arsène* 5303), ×2.



BLAKE on MEIBOMIA

ANATOMY, EMBRYOLOGY, AND ECOLOGY OF ARACHIS HYPOGEA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 325

EDWARD L. REED

(WITH PLATES V, VI, AND ELEVEN FIGURES)

The peanut, which for a number of years has been an important article of food for the peoples of tropical countries, is becoming one of the most important food and feed crops as well as a soil improvement crop in southern United States, where, on account of the ravages of the boll weevil, the agriculturist has been forced to turn to some other plant for a money crop.

Only in the last decade or two has the peanut attained the importance of an agricultural crop. Statistics from the Year-book of the Department of Agriculture show that the average annual import of almonds from 1865 to 1897 increased from 640,530 to 4,020,227 pounds; during the same period the import of filberts and walnuts increased from 3,993,921 to 12,894,106 pounds; while the import of peanuts for the same period fell from 6,522,844 to 149,672 pounds. This is explained by the increase in cultivation in the southern states. The Year-book for 1911 states: "The peanut investigations have caused a rapid extension of the industry. From a beginning of a few hundred acres in 1908, the crop this year will require more than 300,000 acres in the Gulf states alone, where prior to the time mentioned no commercial industry existed."

Before 1879 the acreage of peanuts was insignificant. From 1879 to 1889 the acreage averaged 143,000, and the next three decades show a rapid increase. The decade before 1919 shows an average acreage of 913,000, and over a million acres were planted to peanuts in each of the years 1920 and 1921. The value of the crop in 1920 was $44,256,000. The acreage for 1921 was larger, but owing to a lower price per bushel the value was only $33,097,000. This caused a decrease in the acreage for 1922, but it was still larger than the average for the decade preceding 1919. The value of the 1922 crop was $29,222,000. The value of the peanut crop for the

years 1920–21–22 exceeds that of the bean for the same period. Of thirty field and orchard crops for the years 1920–21–22, seventeen had a greater acreage, one approximately the same, and twelve less than the peanut.

Papers on the peanut have appeared from time to time for the last 300 years, but they were conclusions from too few data, or mere compilations. Very little critical work has been done. Some of the early mistakes have come down through the literature and have crept into one of our best encyclopedias on agriculture and into several of the latest textbooks on southern field crops. It was for the purpose of clearing up some of these points and of making a study of its anatomy, embryology, and ecology that this study was commenced.

Literature

MARCGRAF and PISO (5) were the first to figure the whole plant. Their figure is correct except that it shows no blossoms and represents the nuts as developing on the lateral roots. WALDRON (10) divided the Linnean species into two subspecies, *A. fastigiata* for the erect or bunch type, and *A. procumbens* for the prostrate type. In his description of the types and varieties he speaks of sterile and fertile flowers; while in the description of the bunch type he mentions fertile flowers grouped at the base of the stem, and infers that sterile blossoms are found on the stems and branches higher up.

PETTIT (6) and RICHTER (7) report no root hairs, but WALDRON found them scantily near the tip under favorable conditions, and also found rosettes of root hairs at the bases of newly formed side roots. He found that these rosette hairs had the normal structure of typical root hairs, and that the root tip hairs, when present, were few, short, and scattered, occurring on young, delicate, usually few-branched roots. He found no hairs of either type on the main root. He also found that young elongating roots which bear no root hairs often have their cuticle mucilaginized, causing the soil particles to adhere as if hairs were present. WALDRON states that the mesophyll is composed of two to five-layered palisade tissue immediately below the upper epidermis, and a single layer of water storage cells next to the lower epidermis, and that these features are more typical of a xerophytic plant than is the nature of the stomata. A loose, com-

paratively thin layer of spongy mesophyll separates the palisade and the water storage layers.

In discussing the anatomy of the young gynophore, WALDRON states: "Sections of a gynophore, when very young, show a sessile ovary with usually two parietal ovules. Eleven to thirteen bundles extend from base to tip, branching more or less in their course. Along the inner edge of each bundle are tannin pockets."

Concerning the cambium layer, PETTIT states: "There is an indication of the formation of a cambium ring, although it never occurs even in the oldest portions of the organ." WALDRON considers the meristematic tissue that PETTIT noticed between the bundles to be interfascicular cambium, because he noticed xylem and phloem elements cut off from it to form secondary bundles. He considers the one-celled hairs that develop on the underground portion of the gynophore as absorptive cells simulating root hairs. WINTON (9) in discussing the pericarp, states as follows:

> The pericarp or shell of the peanut, while morphologically corresponding with the pod of other legumes, exhibits some remarkable peculiarities, traceable partly at least to the conditions encountered while ripening in the soil. Not only is it deprived of chlorophyll and consequently of the photosynthetic power of the leaf, but on the other hand it is provided with root hairs, and presumably possesses to some degree the absorptive function of a true root. In other words, the pericarp, although morphologically a leaf, acts physiologically as a root. The epidermal cells are so thin-walled that they are seen with difficulty in surface view. In cross-section, especially after staining with safranin, the presence of typical root hairs arising from the center of many of the epidermal cells is evident. I have been unable to find these hairs on peanuts sold by venders, due probably to their previous removal by cleaning or by friction in the bags, but I have found them on specimens grown in North Carolina.

WALDRON describes the absorptive hairs as "large, unbranched, one-celled, and average nearly one millimeter in length." PETTIT records the cutting off of the root system of a plant, which lived several days without wilting sufficiently to be readily noticed, and suggested that this phenomenon is due to the absorption of water by the gynophore hairs, and adds, "The principal function of the gynophore hair is to furnish a supply of food material for the use of the developing fruit." RICHTER, however, states:

On the underground gynophore section the root hairs are found as a dense case on the whole outer surface. The cross-section of later sections I colored with chlorine-zinc-iodide, and found that the hairs were modified with cork, only on the surface they showed in opposition to the yellow cortex a feeble tinge in the violet of the cellulose membrane. I further treated a number of such sections with concentrated sulphuric acid and found through this reaction likewise a corking of the hairs confirmed. The hairs themselves and even the underlying two or three cork layers remained undecomposed.

Then in a footnote he adds, "Herein the result of my research stands directly opposite to that of STOCKTON-PETTIT." He further suggests that in addition to absorptive organs there is a later function of anchorage for the pod, since later "periderm is formed in the subepidermal layers that bring to an end the absorbing function of the hairs. In still later stages there appears bark structure, which gives the underground gynophore the uneven surface." PETTIT states:

Arachis hypogea is a low annual plant, with one upright flowerless branch surrounded by decumbent spreading branches, upon which flowers are borne. The stem is cylindrical and smooth, at the base becoming angular and hairy above. The stamens are monadelphous and inserted on the calyx. They are ten in number and of two kinds, one with long two-celled anthers dehiscing laterally, and one with nearly spherical one-celled anthers. In the nyctotropic movements of the leaves, ... the main petiole sinks downward, the leaflets twist downward and backward so that the lower surfaces of each pair are applied to each other. In this position they form a little pocket shutting around the petiole, with the superior pair closed over the inferior and the tips pointed upward.

In speaking of the phenomenon of the plant's burying its seeds in the ground, WINTON says, "Shortly after blossoming the flower stalk bends downward until the young fruit is completely buried in the soil." SOLEREDER (8) states:

The hairy covering of the Papilionaceae consists of clothing and glandular hairs. The usual form of the clothing hairs is that of simple uniseriate trichomes with one or several short basal cells and a long terminal cell. Special forms of clothing hairs are as follows; . . . . the multiseriate shaggy hairs of *Aeschynomene*, *Arachis*, *Chapmannia*, etc. Owing to the large number of species in which a mucilaginous epidermis has been demonstrated, usually only the genera concerned can be cited in the following list. The stomata do not belong to one and the same type (Cruciferous), as has been generally assumed (see STRASBURGER and DEBARY). The type with subsidiary cells parallel to the pore (Rubiaceous type) is also very widely distributed.

After discussing the differentiation of the mesophyll and calling special attention to the middle layer that is poor in chlorophyll and is frequently filled with tanniniferous contents, he says that in the leaves of *Chapmannia floridana* and of species of *Arachis*, *Cranocarpus*, etc., the lowest layer of the spongy parenchyma consists of cells with wide lumina and brown contents (in the dried leaf); and that according to TRECUL tannin-sacs occur in the pith in *Adesmia*, *Arachis*, and *Coronella*. He also reports that VOGELBURGER found rod-shaped crystals in species of *Aeschynomene*, *Arachis*, *Chapmannia*, etc. He says that shaggy hairs, filiform multicellular structures, have been observed only in the Hedysareae, namely, in *Aeschynomene*, *Arachis*, and *Chapmannia*.

Materials and methods

The work here reported has been done on *Arachis hypogea*. The plant as a whole has been studied in the laboratory, in the greenhouse, and in the field. Seeds have been germinated and the seedling studied as a whole. Sections have been made by the paraffin method and stained with safranin and light green, and safranin and gentian violet; and living material has been studied. The material was killed and fixed in chromo-acetic acid. Sections from the leaves of field grown plants have been made. Flower buds, freshly opened blossoms, blossoms with withered perianth, and the lengthening gynophore in various stages have been studied. Sections were cut from 5 to 20 μ thick. The developing gynophore has been studied in field conditions, as they exist in the region of crop cultivation in Texas, and in the moist warm conditions of the greenhouse of the University of Chicago. The ecology of the plant as it grows in cultivated regions of Texas has been studied as to maximum and minimum temperature for the fruiting season, also humidity of the air, soil moisture, and wind velocity. Chemical and mechanical analyses of the soil have been made.

Classification and structure

A review of the literature shows that investigators have had various opinions as to the nativity of *Arachis*, Brazil, Africa, China, India, and even Japan having had one or more exponents as the original home. The older DE CANDOLLE (4) has ascribed it to

South America, where all the other species of the genus are found. Evidence seems to point to the fact that it was imported into Africa from Peru, where it was taken from Brazil, and that it was carried from Africa to these countries farther east. It was introduced into the United States during the importation of slaves from Africa, being used as one of the principal articles of food for the negroes on the voyage.

Arachis has not been satisfactorily placed as to its affinities. It seems to belong in the tribe Hedysareae of the Papilionaceae. LINNAEUS placed it next to *Cicer;* PERSOON, nearer *Anthyllis;* JUSSIEU, between *Ononis* and *Anthyllis*. DE CANDOLLE, classifying it according to the character of its embryo, places it among his Geoffroyae, but at the same time, recognizing how little it conforms in other respects to these plants, suggested its forming together with *Voandzeia* a distinct tribe. BROWN says that *Arachis* and *Cercis* possess straight embryos in common with Caesalpineae and Mimoseae, in which respect they differ from the Papilionaceae.

The early botanists, before 1805, all described the structure of the blossom erroneously. The stemlike calyx tube was supposed to be a flower stalk. In 1805 POITEAU published the first correct description of the structure of the blossom. BROWN afterward confirmed POITEAU'S description in 1816. Notwithstanding the work of POITEAU, confirmed by BROWN, BENTHAM (**2**) as late as 1839 writes of *Arachis* as a plant with dimorphic flowers. He describes one form with calyx and corolla, which is always sterile, the fertile flowers having "neither calyx, corolla, nor stamens; but from two bracteolae, similar to those which are formed at the base of the sterile flowers proceeds a stiff rigid stipe or torus, which is speedily reflexed and elongated, and is terminated by what appears to the naked eye a short point. Examined under a glass this point discloses at its extremity a truncated, somewhat concave and dilated stigma."

NEISLER in 1865 found that "the flowers of *Arachis* are all petal-bearing and fertile." BENTHAM remained unconvinced, and published a reply in the same year. What BENTHAM mistook for a cleistogamous blossom was simply the elongated "peg" or gynophore after the blossom parts had fallen off. His stigma was the scar left by the falling off of the style.

Arachis is a low annual with one upright central stem, and numerous lateral, more or less decumbent branches. The central stem, as well as all branches, produces flowers and fruit. Field grown plants, late in the season, not only produce flowers in the leaf axils on the main central stem, but also in the axils of all the branches of this stem. It is not uncommon to find gynophores extending downward from leaf axils as high as 8 or 10 inches from the ground, and a number of peanuts are produced on the main stem in the lower leaf axils. The distinction between the bunch type and the prostrate type is not so clear as the names indicate. It is true that in the prostrate type all branches except the central one are prostrate from the beginning, while in the bunch type the lateral branches at first stand more or less erect; but during the latter part of the season, when the blossoms are being produced abundantly, droop toward the ground and become almost as procumbent as in the prostrate type, and a large number of peanuts are produced on the gynophores from these branches.

LEAF.—The leaf is even pinnately compound, consisting of two pairs of approximately equal leaflets, on a slender petiole of moderate length, and a pair of stipules about 4 cm. long with attenuate points. The stipules are fused with the petiole for about one-half their length. As with most compound leaves, they have nyctotropic movement. The main petiole bends downward and the leaflets move upward until the two upper surfaces are applied to each other, and the two superior leaflets usually inclose the two inferior. The pulvinus instrumental in the nyctotropic movement of the petiole is about 1.5 cm. from the stem, and at the point where the stipules separate from the petiole. My observations on the nyctotropic movements of the leaves do not agree entirely with those which PETTIT records.

As will be shown later, *Arachis* has strong xerophytic tendencies, which make the leaf structure quite striking. Stomata are present on both sides of the leaf in large numbers. They are even with the surface (fig. 1), as in plants having mesophytic characters, and are of average size. It is sparingly pubescent with short hairs. In cross-section (fig. 2) it shows a well developed cuticle, a single layer of epidermal cells, a palisade consisting of two to four layers of cells with numerous intercellular air spaces, a narrow, loosely

arranged sponge tissue, a single layer of water storage cells, and a single layer of epidermal cells with a cuticle which is not so well developed as that on the upper surface. Quite regularly certain cells of the upper epidermis project inward, forming an inverted cone which extends about one-third the diameter of the leaf. These are tannin cells and appear dark brown in stained slides.

STEM.—The stem is cylindrical, hairy, sometimes becoming more or less angular with age. The leaf nodes are usually 2–5 cm. apart. In cross-section the stem shows a large pith, which, in the older portions, owing to the breaking down of the cells, has a tendency to become hollow, this being the way in which hollow stems and stem cavities in general are formed. The epidermis has crystal cells.

ROOT.—*Arachis* has a well developed tap root with numerous laterals, which extend several inches into the ground, with very few near the surface. As a rule, all have the numerous nodules so generally found on leguminous plants. This makes it a valuable plant for rotation if the crop is harvested by pasturing with hogs; but if harvested for the nuts and the hay, as is generally done, the whole plant being removed from the field, very little nitrogen is added to the soil.

The roots are scantily provided with root hairs; in fact, it is very difficult to show that hairs of any kind are formed. As stated, PETTIT and RICHTER failed to find any, but by careful manipulation WALDRON was able to show a few short, poorly developed hairs near the tips of young lateral roots, but none on the main root. He was able to show that rosettes of hairs were developed at the base of lateral roots, and that their growth was stimulated by high temperature and high humidity, and appeared on young plants whose roots grew rapidly, but did not appear later except when the plants showed a renewed growth vigor. The normally produced tip hairs appeared on very young plants whose roots grew rapidly in most air conditions. Saturated heavy soil conditions retarded the growth of the rosette type and inhibited the appearance of the tip hairs. I have been unable to find hairs on the root tips, and but few rosettes on field grown plants, and, since the conditions under which WALDRON was able to produce them are seldom met with in the field, it is doubtful whether they are normally produced in crop cultiva-

tion, and, when produced, are so few as to be of no practical value to the plant in the absorption of food materials. When we know that the leaf has characters typical of mesophytic plants with only a few xerophytic characters, it is difficult to explain how the plant grows so well and fruits so abundantly in the driest portion of our southern summers. Cross-sections of the root show that it is typically dicotyledonous.

FLOWER.—All flowers are complete and are produced both above and below the ground, singly or in clusters of about three in the axils of the leaves. In field cultivated plants it is not uncommon to find blossoms with yellow petals 3 inches below the surface of the soil.

The calyx is synsepalous, having a tube about an inch long crowned by five irregular calyx tips. It was this long calyx tube that the early botanists mistook for a peduncle; hence their error in describing the plant.

The corolla consists of five irregular yellow petals, typically papilionaceous, inserted on the throat of the calyx tube.

The androecium consists of ten monadelphous stamens, the filaments of which are fused into a tube for about two-thirds of their length. Eight are anther bearing, the two sterile ones being fused with a neighboring filament for almost their entire length. Sometimes only nine are discernible. There are two kinds of anthers, four long two-loculed dehiscing longitudinally, and four round one-loculed. Sections of anthers show that not all of the pollen grains develop completely. The abortive pollen grains with the reduction in the number of anthers is what one would expect in a plant that has close pollination and shows progress toward true cleistogamy.

The pistil is sessile and consists of a single carpel. The style is curved upward, bearded near the tip, and terminated with a stigma. A longitudinal section shows one locule and one to five ovules with constrictions of the ovary wall between them.

Seed and seedling

An examination of a mature seed shows it to be a straight embryo, consisting of two fleshy cotyledons, a short hypocotyl, and a plumule, the latter composed of a terminal and two lateral buds, the whole inclosed within a thin testa. These three buds are well

developed when the seed is mature, and consist of two or more compound leaves. The reserve food stored within the seed consists approximately of 26 per cent protein, 38 per cent oil, and 24 per cent starch, sugar, etc.

In germinating, the hypocotyl elongates and the cotyledons are raised above the ground. The terminal bud develops more rapidly than the lateral ones, but all three grow so that from the beginning the young plant has three principal branches. This is of especial advantage to the bunch type in which such a large percentage of the nuts is produced in the lower leaf axils. The terminal branch continues in an upright position, while the lateral and all secondary branches are more or less decumbent or spreading.

Embryo sac

The embryo sac is oval, with the antipodal end tapering and bent slightly toward the chalazal side. It is filled with starch grains in such quantity that it is difficult to see the nuclei (fig. 3), which in the mature embryo sac are eight in number. The egg apparatus and antipodals are normally placed, the latter soon disintegrating so that it is difficult to find them (fig. 4). After fertilization the endosperm nucleus rapidly divides, forming a great number of free nuclei which arrange themselves against the wall. Cell walls are not immediately formed around these, except near the egg apparatus (fig. 5). The starch grains previously mentioned disappear, having been utilized as food for the developing endosperm nuclei. The embryo sac now consists of a large cavity filled with a homogeneous fluid surrounded by a layer of nuclei held together by a rather dense mass of cytoplasm. As the embryo develops, walls are formed around the remaining nuclei, thus forming a single layer of cells lining the sac, which is the only tissue formed by the endosperm nucleus. This layer of cells lying between the embryo and the wall corresponds to the single layer of endosperm cells left between the developing embryo of the sunflower seed and its wall when the other parts of the endosperm are used as food.

Development of embryo

The egg on germinating divides horizontally, forming a two-celled body just as if it were going to form a suspensor of a single layer of cells (fig. 5), but in further development the divisions are in

three planes, and a suspensor is formed having, in optical view, two rows of cells (fig. 6). At this stage it is easy to distinguish the embryo-forming region from the suspensor by its smaller cells and denser protoplasm, and, as development continues, a longer suspensor is produced, which is no larger in diameter (fig. 7), however, pushing the embryo region farther into the sac. Up to this time there is very little enlargement of the embryo portion; but, as this region develops, the suspensor enlarges, becomes sagittate, with the narrowest portion four or five cells in diameter, which gradually expands to its union with the embryo (fig. 8), and the point becomes sharp, pushing its way among the cells of the nucellus (figs. 9, 10).

The large size of the cells of the suspensor is quite noticeable when compared with those of the proembryo, and should no doubt be explained physiologically as an adaptation that aids in the rapid transfer of food from the nucellus to the embryo, since there are fewer cell walls to be traversed. The nature of the cells of the nucellus which surrounds the suspensor adds weight to this interpretation, since the suspensor is kept closely appressed to the wall of the embryo sac, the cells of which are elongated and arranged in rows more or less at right angles to its surface (figs. 6, 8, 9, 10). These serve as food conducting tissue, carrying the digested food of the nucellus and ovule wall to the suspensor.

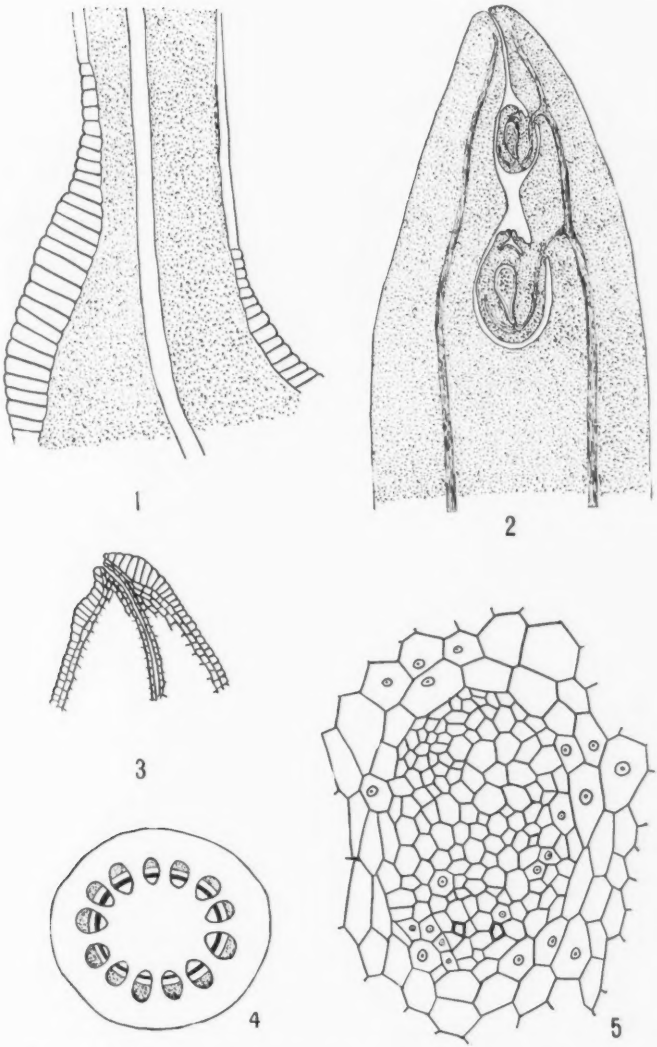
There are three different groups of cells in the ovule wall: (1) Those immediately surrounding the vascular bundles, which are small, having dense protoplasm and relatively larger nuclei than those of the other two groups, and which serve as conducting tissue, carrying transported food to the storage region. (2) The storage region, consisting of large cells in which abundance of starch grains are found. (3) The food conducting region, which lies next to the embryo sac. With the exception of the rows of elongated cells of the nucellus at the micropylar end, the food conducting region consists of one or two rows surrounding the sac (figs. 10–12). The storage region comprises by far the greater portion of the ovule wall, and the density of the reserve food increases from the outside inward, reaching its maximum near the inner wall. The two or three rows of storage cells lying next to the conducting region show but few starch grains, due to their rapid digestion and absorption (fig. 11).

The first indications of the embryo are to be seen in two swellings, the cotyledonary primordia (fig. 13), at opposite points in the proembryo, due to accelerated growth at these points. These primordia soon develop into diverging projections, between which is the stem tip initial (fig. 10). As development proceeds, the enlarging cotyledons become closely approximated, being forced together by the walls of the sac (fig. 12). Between them is the plumule, consisting of a terminal bud and two lateral ones developed in the axils of the cotyledons, thus forming a complex plumule. These buds are well developed, and are composed of two or more compound leaves; therefore, in germinating, the plumule expands into typical leaves of the adult plant. The short hypocotyl is the last to make its appearance, its tip developing at the top and a little to one side of the center of the massive suspensor (figs. 10–12). The mature seed occupies the entire space within the integument, and is a straight embryo.

Gynophore

As soon as fertilization is accomplished, the internode between the ovary and the receptacle begins to elongate, and soon turns downward at such an angle to the stem as to reach the earth in the shortest distance. The magnitude of the angle, therefore, is determined by the magnitude of the angle formed by the stem and the earth. This elongation is produced by a region of meristematic tissue lying just behind the ovary, the central region forming the pith, and the peripheral the vascular bundles and the cortex. The tip of the ovary becomes pronounced by the elongation and lignifying of a group of epidermal cells, which in their development push the base of the style to one side and form a cap analogous to a root cap (text fig. 1).

As soon as the gynophore has pierced the ground to a depth of 2–5 cm., the ovary, which up to this time has remained dormant, begins to develop, the end of the gynophore becomes swollen, and, by unequal growth on the side next to the base of the plant the ovary takes a horizontal position, so that the two or more ovules come to lie in the same straight line parallel to the surface of the earth. The lower ovule develops first, followed by the others in succession, so that, if any one fails to develop, it is usually the one in the end of the ovary.



FIGS. 1–5.—Fig. 1, tip of ovary forming cap by elongation and lignifying of epidermal cells; fig. 2, longitudinal section of gynophore showing one locule with two anatropous ovules; fig. 3, cap formed by elongated lignified epidermal cells; fig. 4, diagrammatic drawing of cross-section of gynophore; fig. 5, cross-section of very young bundle with no sign of cambium.

DARWIN (3) has shown that the growth downward of the gynophore is not due to negative phototropism, and infers that it is due to positive geotropism, and WALDRON found some granules in the lumen of the tip cells and suggests that their presence stimulates positive geotropic movement. Sometimes if the gynophore fails to reach the ground, due to the distance that the flower is from it, the ovary will begin growth and form an enlargement at the tip and then develop chlorophyll, but it never matures seed. The development of chlorophyll by an ovary that has failed to reach the ground, and by those that have been exposed to light by the removal of the soil, shows the retention of functional chloroplasts after long periods of disuse.

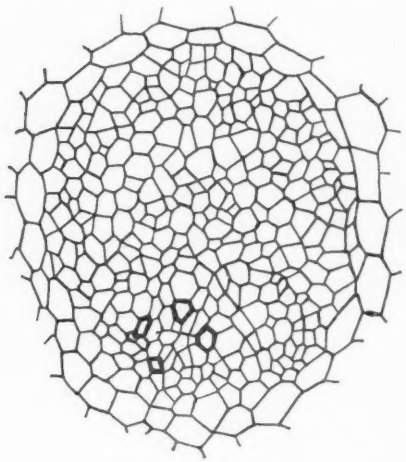


FIG. 6.—Section of older bundle with enlarged cells just beyond xylem strands, cambium initials.

A longitudinal section of the tip of a gynophore shows well developed vascular strands, one locule, and anatropus ovules (text fig. 2). The base of the style is pushed to one side by the development of elongated epidermal cells, which form a protection for the delicate tip while piercing the ground (text fig. 3). Text fig. 4 is a cross-section of a mature gynophore, showing a large pith, a vascular ring of thirteen bundles, and a cortex. While eleven to thirteen are the usual numbers for vascular bundles, however, it is not uncommon to find as many as fifteen or more, due to the action of interfascicular cambium. A cross-section of a very young bundle shows no sign of cambium and only a few xylem strands, the whole being surrounded by large cortex and pith cells (text fig. 5). A cross-section of an older bundle shows a group of thin walled cells just beyond the xylem strands; these are the cambium initials (text fig. 6). Text fig. 7 shows mitosis in one

of the cambium initials forming the first cambium cells, while text fig. 8 is of a still older bundle in which the cambium has formed almost completely across. Text fig. 9 is of a mature bundle with well developed xylem, cambium, phloem, a large lignified bast, and interfascicular cambium.

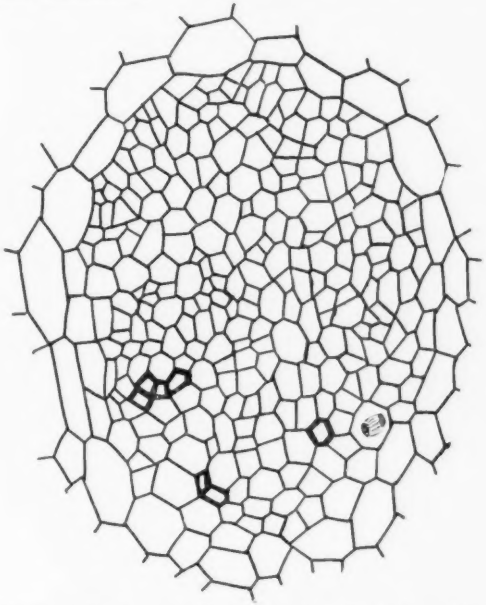


FIG. 7.—Cross-section of young bundle showing mitosis in cambium initials

Ecology

The plot studied during the season of 1923 was about one-tenth of an acre. The nuts were carefully shelled before planting, and no seed with a broken testa was used. The rows were 1 m. apart, and the seeds were planted every 15 cm. in the row. The plot, a fine sandy loam, was planted the first week of May, this being the usual time of planting in this section of Texas. In about ten days the young plants were all through the ground with practically 100 per cent germination. They grew vigorously, and soon had strong upright branches with smaller lateral branches from the axils of the cotyledons.

SOIL.—Geologically, the soil is known as Windthorst fine sandy loam, and is low in nitrogen, total phosphoric acid, and in active phosphoric acid; it is neither acid nor alkali. It is 8–12 inches deep, with a red to yellowish clay subsoil. Surface drainage is good, but drainage by percolation is poor. The types of vegetation

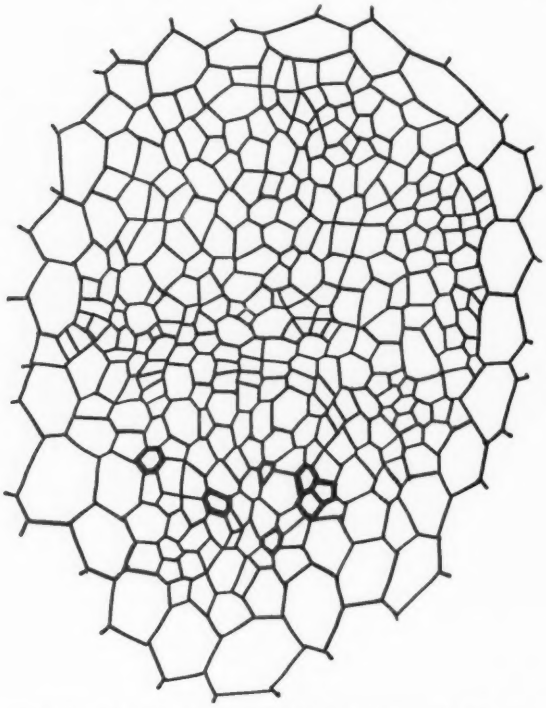


FIG. 8.—Section of bundle showing cambium almost completely across

found on unbroken Windthorst fine sandy loam in this immediate vicinity are mesophytic and xerophytic, since this is a transition zone between the mesophytic region of the eastern portion of the state and the xerophytic portion of the western plains.

RAINFALL.—The rainfall was measured by a standard rain gauge of the Weather Bureau type, located about 20 feet from the western edge of the plot. Text fig. 10 shows the rainfall from April 1 to Sep-

tember 13. Since the rainfall for April was 3.62 inches, the soil was in good condition as to moisture when the seeds were planted. The small rainfall of only 0.51 inches in May permitted the soil to dry to such an extent that truck and garden crops in the immediate vicinity suffered, but its effect upon the peanuts was scarcely noticeable. During the first thirteen days of June the rainfall

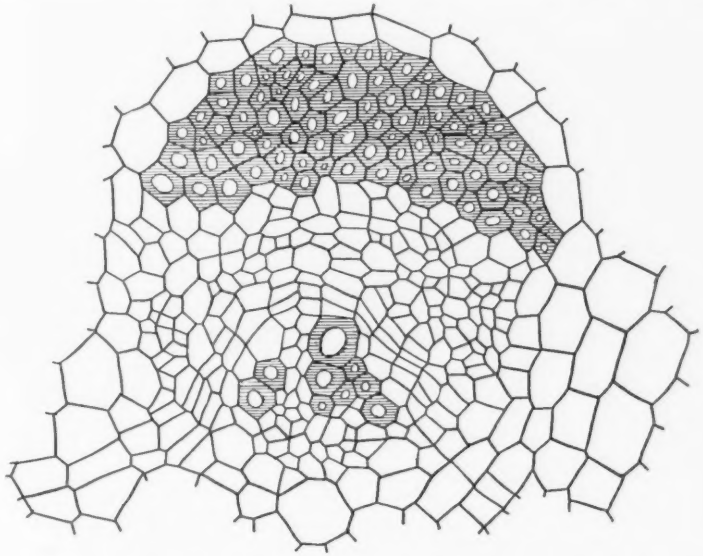


FIG. 9.—Cross-section of nearly mature bundle showing xylem, cambium, phloem, and lignified bast; cambium extends beyond limit of bundle and is, therefore, interfascicular cambium.

was 2.88 inches, and this was followed by a period of ninety-six days, ending September 14, in which the precipitation was only 2.25 inches, with the greatest single rainfall of 0.96 inches on July 1 and the second greatest of 0.80 inches on August 27. This amount of rainfall is insufficient for normal crop production, and most farm and truck crops suffered considerably, with the yield materially reduced. June corn due to fruit during this period produced from one-third to one-half crop. The peanuts on the plot and those in field cultivation on the College Farm about one and one-half miles

distant were not materially affected, although this was the period of blossoming and setting of fruit. From September 15 to September 18 inclusive there was a rainfall of 2.70 inches, and no more rain fell until after the crop was harvested on October 1, at which time there were but few immatured nuts on the vines. A few plants were left in the field and were harvested on November 30, but these

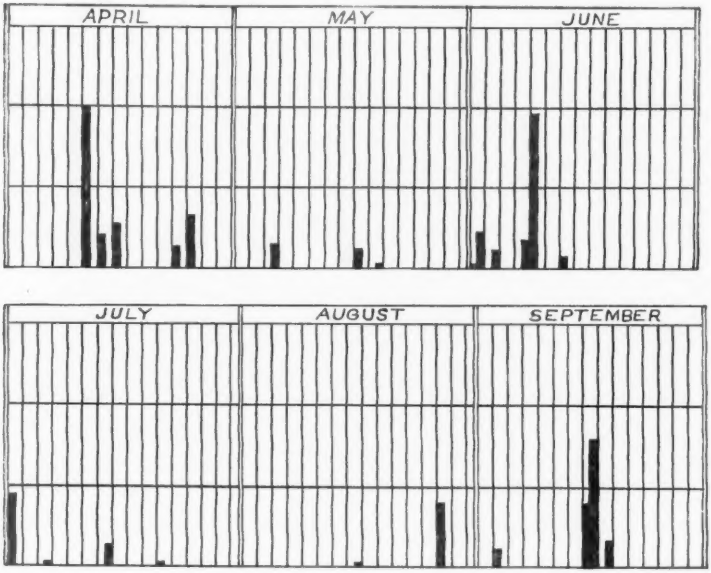


FIG. 10.—Graph of soil moisture content during fruiting period

showed no increase in number of nuts, showing that the main crop was produced during the period of light rainfall.

Table I shows the dates on which soil samples were taken, the depth in centimeters, and the percentage of water in terms of dry soil. Two depths were used: 5 cm., the depth in which the nuts are generally ripened, and 15 cm., the depth of the main root system. Text fig. 11 shows these percentages graphically. The soil samples were taken during the period in which the crop was produced, that is, from July 25 to September 15. Thus the upper 5 cm. of soil, that in which the main crop of nuts was produced, was exceedingly

deficient in moisture, and the soil in which the main body of roots grew was not abundantly supplied with water. The wilting coefficient of the soil, determined by growing peanuts, Indian corn, and tomatoes in pots, is about 2.5 per cent.

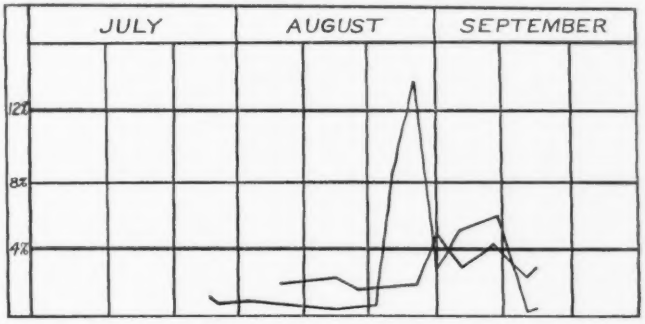


FIG. 11.—Graph of rainfall during month preceding time of planting and during growing season.

TABLE I

WATER CONTENT OF SOIL SAMPLES FROM FIELD IN WHICH PLANTS WERE GROWN

Date	Depth (cm.)	Percentage water	Date	Depth (cm.)	Percentage water
July 25	5	0.99	August 27	5	13.70
July 25	5	0.76	August 31	15	4.30
July 28	5	0.64	August 31	5	2.40
August 3	5	0.67	September 4	5	5.10
August 6	15	1.80	September 4	15	2.70
August 15	15	2.00	September 9	5	5.90
August 15	5	0.48	September 9	15	4.10
August 18	15	1.30	September 13	15	2.00
August 21	15	1.30	September 13	2.5	0.22
August 21	5	0.51	September 15	2.5	0.77
August 23	5	9.90	September 15	15	2.80
August 27	15	1.60			

WALDRON, WINTON, PETTIT, and RICHTER regard the hairs on that portion of the gynophore which is underground as absorptive hairs, absorbing water and food material for the plant in general, or for the developing fruit. Since the ground in which the fruit is developed has such a small percentage of water, and since it is difficult to find these hairs on normal field grown plants, it is very improbable that the peanut is affected to any great extent by the

presence of hairs on the gynophore. The plot under the climatic conditions here given produced a crop of about 20 bushels per acre, which is considered normal for such soils.

METEORIC CONDITIONS.—Table II gives the meteoric conditions during the month preceding the planting time and for the four months during which the plants grew. The number of clear days for the four months was 123, of partly cloudy 12, and of cloudy 9; hence there was a great predominance of clear weather. Table III shows the velocity and direction of the prevailing wind. For

TABLE II

METEORIC CONDITIONS DURING PERIOD OF GROWTH

Month	Number of days clear	Number of days partly cloudy	Number of days cloudy
April	16	9	5
May	27	4	0
June	22	3	5
July	28	1	2
August	25	4	2

TABLE III

VELOCITY AND DIRECTION OF PREVAILING WIND

Month	Average velocity per day	Average velocity per hour	Direction of prevailing wind
May	142.0	6.0	South
June	113.0	4.7	16 north 10 south
July	65.6	2.7	North
August 1–September 21	74.0	3.0	South

May the average velocity was six miles per hour, for June four and seventh-tenth miles, for July two and seven-tenth miles, and from August 1 to September 21 it was three miles per hour. During May, one-third of June, and from August 1 to September 21 the prevailing wind was from the south. Table IV shows the temperatures for the month preceding the time of planting and for the four months during which the crop grew and set fruit. From the time of planting to the time of harvest there was a gradual increase in maximum and minimum temperatures, with a corresponding decrease in range, and the high means with the velocity and direction of the prevailing wind indicate a high rate of transpiration. It is difficult to explain the ability of the peanut plant to thrive so

well with the mesophytic nature of its leaf structure in a region with the climatic conditions as they exist here.

TABLE IV

TEMPERATURES FOR GROWING AND FRUITING PERIOD

Month	Maximum	Minimum	Mean maximum	Mean minimum	Mean	Range
April	80	38	61.2	46.3	53.7	42
May	99	45	73.2	51.8	65.5	54
June	103	51	86.8	65.7	76.2	52
July	104	62	92.7	69.8	81.2	42
August 1–15	105	68	102.6	71.3	86.9	37

Summary

1. *Arachis hypogea* is a native of Brazil, but its wild ancestor is not known. While it is a member of the Leguminosae, it has not been definitely placed as to its affinities.

2. It is a low annual which, by a lengthening of the internode just below the ovary, pushes its pod below the surface of the soil where the seeds are ripened.

3. The root system is that of the tap root type. Root hairs are of two kinds, normal root tip hairs, and rosettes at the base of the lateral roots. The hairs are so scantily developed in field grown plants that their influence as absorptive organs is negligible.

4. The seed is a straight embryo, and consists of two large cotyledons, a short hypocotyl, and a plumule composed of a terminal and two lateral buds.

5. The mature embryo sac has eight nuclei and numerous starch grains. The antipodals soon disappear. The endosperm nucleus forms numerous free nuclei, which later form a single layer of cells lining the sac.

6. The fertilized egg produces a massive proembryo, which early differentiates into the embryo region and the suspensor.

7. The gynophore has typical stem structure. There is a large pith, about thirteen vascular bundles, both fascicular and interfascicular cambium, and a cortex. It responds to positive geotropism.

8. It grows well and fruits abundantly in hot, relatively dry climates, although the leaves are typically mesophytic with a few xerophytic characters.

I am greatly indebted to Professor W. J. G. LAND, under whose direction the work was done, and to Professors H. C. COWLES and G. D. FULLER for helpful suggestions.

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EXPLANATION OF PLATES V, VI

FIG. 1.—Section through stoma, showing location at surface of leaf.

FIG. 2.—Section of leaf, showing open arrangement of palisade, small open sponge, single layer of water storage cell, tannin sac, and epidermis consisting of single layer of cells.

FIG. 3.—Embryo sac with two nuclei and mass of starch grains.

FIG. 4.—Embryo sac, showing egg apparatus and two polar nuclei.

FIG. 5.—Embryo sac with free nuclei against wall; synergids at antipodal end, fertilized egg divided once, and cell walls formed around nuclei in vicinity of egg.

FIG. 6.—Proembryo with neighboring nucellus cells; embryo-forming cells distinguished from suspensor by denser protoplasm and smaller cells.

FIG. 7.—Older proembryo with longer suspensor.

FIG. 8.—Still older proembryo with embryo-forming region enlarging; arrangement of nucellus cells also shown.

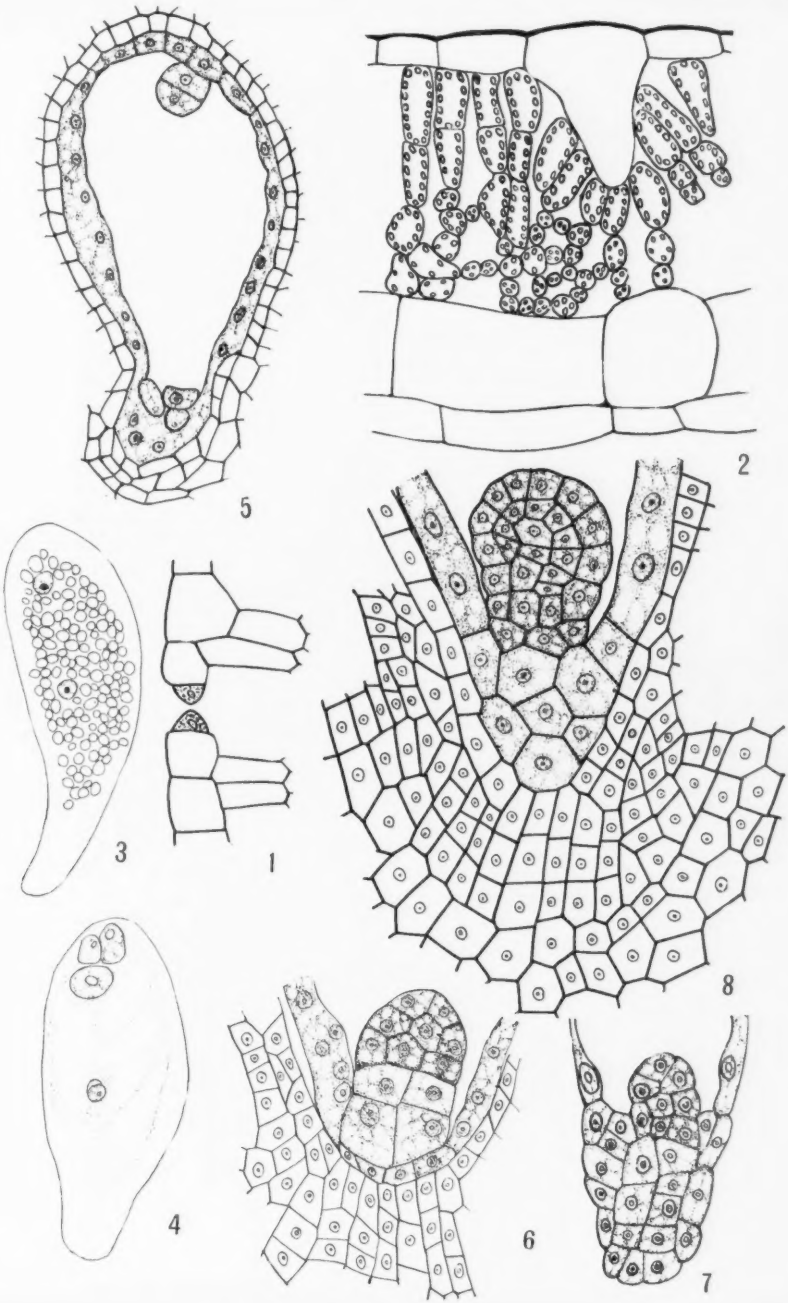
FIG. 9.—Point of suspensor and its relation to food conducting region of nucellus.

FIG. 10.—Stem tip, root tip, elongating cotyledons, and sagittate suspensor; also food conducting region at micropylar end of embryo sac.

FIG. 11.—Foot of older suspensor than in fig. 9, with portion of storage region.

FIG. 12.—Longitudinal section of ovule, showing three regions of ovary wall (vascular, storage, and conducting regions).

FIG. 13.—Primordia of cotyledons.



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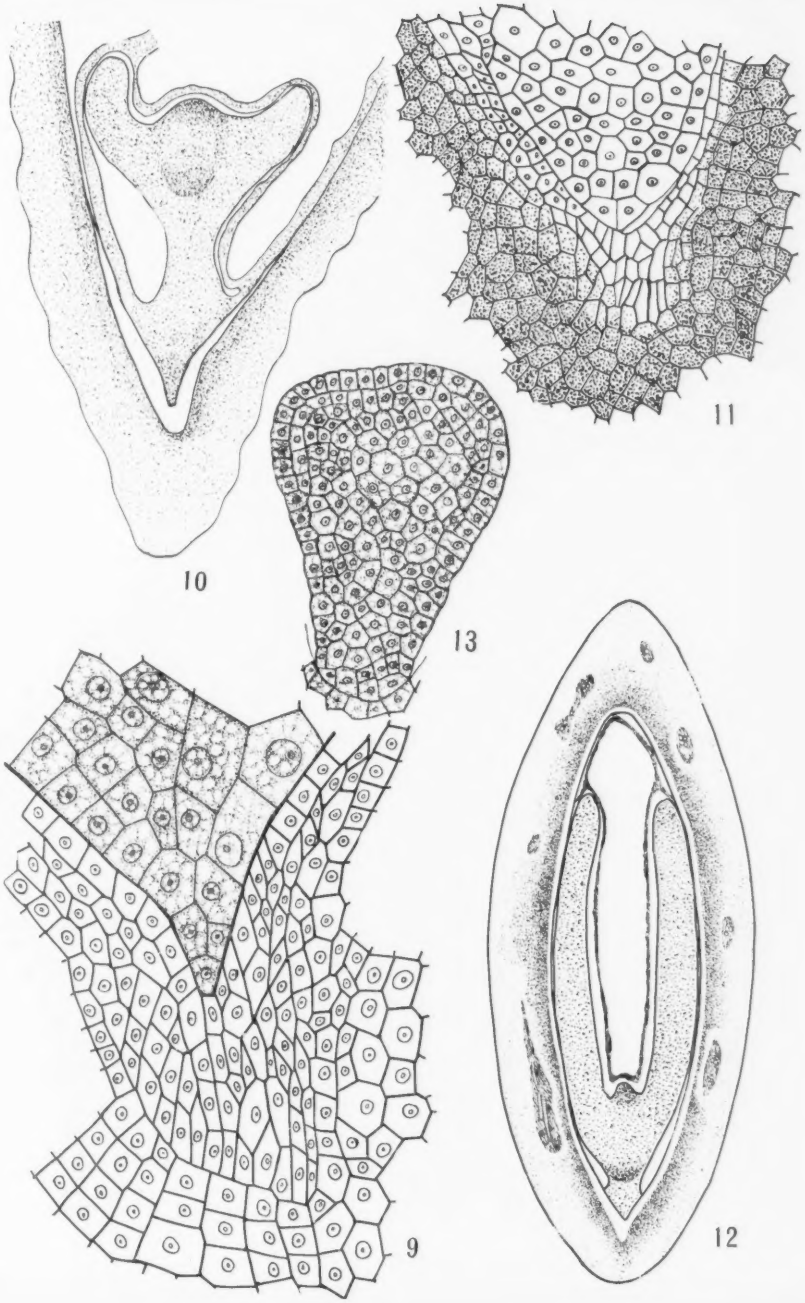

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RELATION OF LOW TEMPERATURES TO RESPIRATION AND CARBOHYDRATE CHANGES IN POTATO TUBERS[1]

E. F. HOPKINS

(WITH SEVEN FIGURES)

It is well known that respiration, like other physiological processes, is greatly influenced by temperature. The literature on this subject is discussed by GORE (**7**), and more recently by CZAPEK (**5**). The general conclusion is that, for a certain temperature interval at least, respiration in plants increases with temperature according to the empirical rule of VAN'T HOFF, which was first applied to purely chemical reactions. This rule states that for every rise of 10° C. the respiratory rate is doubled or trebled.

Besides the direct effect of temperature on respiration, it is also believed by PALLADIN (**12**) that there is a stimulating effect caused by temperature changes. He obtained a large increase in respiration intensity in the case of bean seedlings, by exposure both to low temperature and to high, after returning them to the original temperature. Little consideration, however, has been given to the effect of continuous holding at the lower temperatures on respiratory activity, and of course this is of importance in connection with cold storage, besides having perhaps some theoretical interest.

In the case of potato tubers it was found by ZIEGENBEIN (**16**) that as the temperature was lowered from 45° C. to 10° C., the respiration fell to a very low value. It is generally considered that the respiration at 0° C. is practically nil (**1**). In order to gain more information concerning physiological activities at temperatures below 10° C., a somewhat detailed study has been made.

Methods

The apparatus described by GORE (**7**), somewhat modified, was used, a large desiccator serving as the respiratory chamber.

[1] Contribution from the Marble Laboratory. The writer wishes to express his thanks to Mr. L. M. MARBLE for his interest in the work, and to Dr. LEWIS KNUDSON for reading the manuscript.

The carbon dioxide absorption was carried out in Reiset absorption tubes, and when samples were not being collected the outlet from the desiccator was connected to the suction, so as to allow a constant current of air to flow through the apparatus. The usual precautions to assure complete absorption of the CO_2 evolved and to prevent atmospheric carbon dioxide from entering the respiratory chamber were taken. About 4–5 kg. of potatoes were used, and samples were taken for about five hours at certain intervals. The results in each case were calculated to milligrams of carbon dioxide per kilogram hour.

The carbon dioxide was estimated as follows. The gas was absorbed in 100 cc. of N/5 NaOH, free from carbonate, in the Reiset tube mentioned. The walls were then rinsed with several portions of distilled water, which were allowed to run into the filter flask. Titration was carried out with N/2 HCl in the same vessel, after adding an excess of barium chloride solution and about 40 cc. of neutral 95 per cent alcohol. Orthocresolphthalein as recommended by CLARK and LUBS (4) was used as an indicator, and very sharp end points were obtained. The addition of the alcohol increased the sharpness of the end point, especially when considerable barium carbonate was present, and this was considered to be due to the fact that the dissociation of the $BaCO_3$ in the presence of alcohol is very small. This method the writer believes is preferable to the double titration method using phenolphthalein and methyl orange, where the end points in both cases are uncertain and empirical. The exact strength of the NaOH solution need not be known, as the amount of CO_2 can be calculated from the HCl solution, which is easily and accurately standardized gravimetrically by means of silver chloride.

The sample titration of a solution of sodium bicarbonate shown in table I gives an idea of the accuracy for small amounts of CO_2. Ten cc. of a weak $NaHCO_3$ solution was added to each of the determinations, and may be considered as equivalent to a certain amount of CO_2. None was added to the blanks. The difference in the back titration with N/2 HCl between the determinations and the blanks, therefore, is equivalent to the number of milligrams of CO_2

as shown. Much larger amounts were determined in the actual analyses and the percentage of accuracy much greater.

TABLE I

ACCURACY OF TITRATION METHOD FOR CO_2

	BLANKS		DETERMINATIONS			
	I	II	I	II	III	IV
Back titration cc. N/2 HCl	41.44	41.41	40.89	40.91	40.94	40.90
Titration less blank cc	.....	.....	0.53	0.51	0.48	0.52
Equivalent to mg. CO_2	.....	.....	5.8	5.6	5.3	5.7

Experiments

EXPERIMENT I.—The first experiment was carried out at two temperatures, 0° C. (32° F.) and 4.4° C. (40° F.). American Giant tubers were used, and were carefully selected as to uniformity in shape and size, and as to freedom from injuries, rots, etc. The apparatus was set up in duplicate for each temperature, in cold storage rooms where the variation in temperature amounted to about 1° C. The potatoes had previously been placed in these rooms November 23, 1922, from the cellar storage, where the temperature at the time averaged about 10° C. (50° F.). The data are summarized in table II.

TABLE II

RESPIRATION OF TUBERS AT 32° AND 40° F.

Date	11/28	11/29	12/1	12/4	12/5	12/6	12/7	12/8	12/9	12/12	12/15	12/18	12/22	1/3	1/17	1/20
Milligrams CO_2 per kg. per hour 0° C.	5.6	2.9	4.7	5.3	5.6	4.9	5.8	6.3	6.2	7.5	6.8	4.9	4.2	3.8	3.7	3.3
Milligrams CO_2 per kg. per hour 4.4° C.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	3.5	2.0	2.3	2.3	2.7	2.5

It will be noted that the respiration at 0° C. (32° F.) is greater than at 4.4° C. (40° F.). For the time during which the two tests coincide, the average respiration at 4.4° C. is only about 60 per cent of what it is at 0° C. (32° F.). Fig. 1 shows this very clearly, and also that the respiration at these temperatures is not constant, but varies with the time until perhaps an equilibrium condition is reached. The respiration at 0° C. is seen to pass through a maxi-

mum at which considerable carbon dioxide is evolved, and then to again approach its original value. This phenomenon is the opposite of what we should expect from our previous knowledge of the effect of temperature on respiration. In other words, the respiratory activity should be very weak at the freezing point of water. The anomaly, however, is perhaps explicable if we accept the hypothesis of PALLADIN (12), previously mentioned, that for every temperature change there is stimulation of respiration; and that in this case this effect is great enough to show itself above the

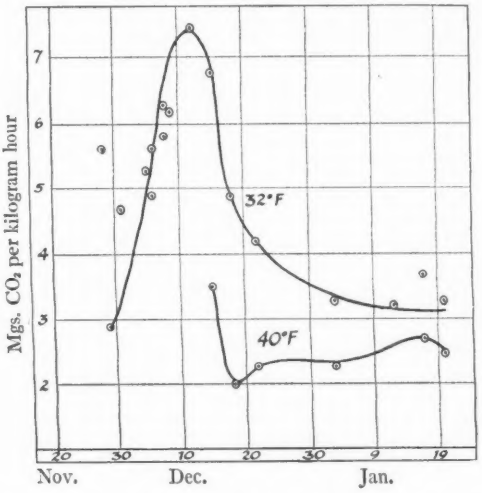

FIG. 1.—Respiration of tubers of American Giant potatoes at 32° and 40° F. plotted against time.

retarding effect of the low temperature on the purely chemical reaction. It is obvious, if these data can be verified, that, as was previously suggested by GORE (7), the Van't Hoff rule will not hold at low temperatures; but the cause would not be the injurious effect of the cold, but its stimulatory effect, and the temperature coefficient would be larger instead of smaller than calculated. The researches of MÜLLER-THURGAU (10) and others (1, 3) on the accumulation of sugar in storage organs at the expense of starch, when held at low temperatures, show that diastatic action must be stimulated at the freezing point. This is a similar phenomenon,

and therefore it appears that we are dealing with a physiological response, and not merely a chemical reaction. PFEFFER (14) has discussed this point, and states "that the action of temperature is mainly a stimulatory one, and that a change of temperature affects metabolism in a manner corresponding to the reactive power of the organism itself. . . . . The physiological curve and the curve of chemical reaction hence do not coincide."

The final retarding of the respiration rate may be caused by the accumulation of certain products which inhibit the reaction. This would be analogous to the decrease of sugar accumulation in potatoes at low temperatures (APPLEMAN 1), and to the inhibition of diastatic action in fungi by the addition of cane or grape sugar, as reported by KATZ (8).

EXPERIMENT II.—In this series three kinds of tubers were used, American Giant, mature Irish Cobblers, and second crop Irish Cobblers. The respiration was determined in duplicate in each case for about five days, and the average result per kilogram per hour calculated. The temperature was then lowered five Fahren-

TABLE III

EFFECT OF TEMPERATURE ON RESPIRATION OF TUBERS OF AMERICAN GIANT, MATURE IRISH COBBLERS, AND SECOND CROP IRISH COBBLERS

TEMPERATURE	RESPIRATION IN MG. PER KILOGRAM PER HOUR		
	American Giant	Cobblers mature	Cobblers second crop
0° C. (32° F.)	4.22	5.04	2.83
1.67° C. (35° F.) . . .	3.77	4.41	1.99
4.4° C. (40° F.)	3.26	5.10	2.36
7.2° C. (45° F.)	4.14	6.00	3.09
10° C. (50° F.)	5.12	8.02	3.37
12.8° C. (55° F.) . . .	6.55	9.02	4.28

heit degrees, and after allowing a day or so for the potatoes, apparatus, etc., to come to temperature, the evolution of CO_2 was again determined.

While there may be certain objections to carrying out the experiment in this manner, the data are interesting and show at least two things: first, that there is a difference in intensity of respiration, depending on the variety and maturity of the tubers; and second,

that the value at 0° C. is greater in each case than at 1.67° C. (35° F.), and in two instances is greater than at 4.4° C. (40° F.). This latter is in keeping with the results of the previous experiment. The data are shown in table III.

EXPERIMENT III.—In order to check these results, another experiment was performed, in which the respiration of tubers of the Russett Rural variety were studied at eight different temperatures. With one exception the temperatures were maintained, as

TABLE IV

INFLUENCE OF TEMPERATURE ON RESPIRATION OF TUBERS OF RUSSETT RURAL; IN MG. CO_2 PER KG. PER HOUR

Average temperature	3/10/23	3/12	3/14	3/16	3/19	3/21	3/23	3/26	3/28	3/31	4/2	4/4	Average
−0.83° C. (30.5° F.)	1.0	1.6	2.1	2.0	1.7	1.8	1.8	3.0	3.0	2.8	2.1	2.0	2.07
+0.22° C. (32.4° F.)	2.4	2.8	5.2	5.7	4.8	4.4	4.2	.....	.....	4.1	3.1	3.2	3.99
1.17° C. (34.1° F.)	1.8	1.8	2.3	2.8	2.5	2.2	2.3	2.1	2.1	2.3	2.4	2.4	2.25
3.06° C. (37.4° F.)	2.5	2.3	2.8	3.0	2.1	1.8	1.2	2.2	1.9	2.0	2.1	2.1	2.14
4.5° C. (40.1° F.)	3.0	2.8	3.4	2.6	2.3	2.3	2.2	2.4	2.3	2.1	2.2	2.0	2.47
6.72° C. (44.1° F.)	2.8	2.9	3.5	3.1	2.8	2.3	2.2	2.7	2.7	2.8	2.7	2.6	2.76
8.67° C. (47.6° F.)	.....	.....	3.2	3.2	2.4	4.8	3.6	3.6	3.1	3.3	.....	2.9	3.34
11.5° C. (52.7° F.)	7.7	7.0	7.8	8.6	4.7	5.7	5.1	5.4	3.7	4.7	5.3	4.5	5.87

before, in cold storage rooms, and the range of variation was about 1°. A cold water bath was utilized to obtain a temperature of 8.89° C. (48° F.). In this case the temperature varied about 1° C. The tubers were taken from cellar storage, where the temperature had been fairly constant for some time at about 4.4° C. (40° F.). The apparatus was set up in duplicate at each temperature, and the absorption and titration carried out as before. The results are presented in table IV.

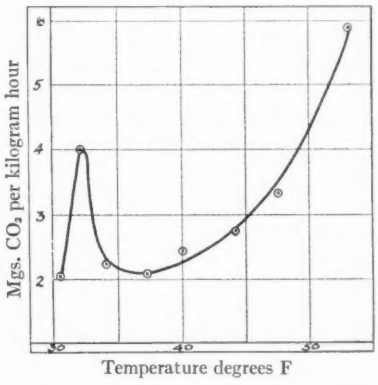

FIG. 2.—Respiration of tubers of Russett Rural potatoes at various temperatures.

The curve plotted from the average of the results over the period is shown in fig. 2. The data at any given date if plotted show a very similar type of curve, although the effect due to the acceleration at 0.22° C. (32.4° F.) is more marked for the earlier

analyses. It is evident from this curve that physiological activity, as determined by respiration, is at a low point at about 3.0° C. (37.4° F.), increases rapidly as the temperature is raised to 11.5° C. (52.7° F.), and also as it is lowered to 0° C. It declines again at −0.83° C. (30.5° F.). The complete explanation of this result is difficult; increase with increasing temperature is to be expected. The increases at 0° C. may be due to stimulation, as discussed previously, while the decrease at −0.83° C. may perhaps be due

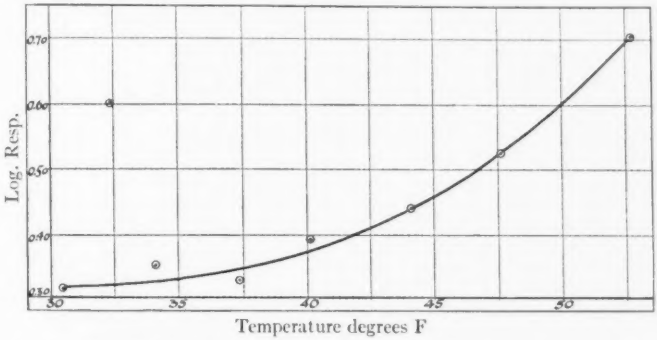

FIG. 3.—Logarithms of respiratory values plotted against temperature; Russett Rural variety.

either to the retarding effect of the low temperature on chemical reactions, or to injury of the tissue. If the logarithms of the figures representing the amounts of carbon dioxide evolved from −0.83° C.–11.5° C. are plotted against the temperature (fig. 3), a smooth curved line is obtained if we neglect the value for 0° C. The curve appears to approach a straight line at its upper extremity.

The respiration plotted against time is shown in fig. 4 for three temperatures. Acceleration of respiration at 0° C. was again observed, while at −0.83° and 4.5° C. there is slight increase, if any.

Carbohydrate changes

The accumulation of sugar in potato tubers stored at low temperatures, and its subsequent disappearance when they are again returned to higher temperatures, has been shown by MÜLLER-THURGAU (10), and later by APPLEMAN (1). The former has suggested also that respiration is markedly affected by the changes due

to the variation in the sugar content, and BUTLER interprets his data as showing that respiratory activity of potatoes is more influenced by the amount of sugar than by temperature. It was thought that perhaps a correlation could be found between the sugar con-

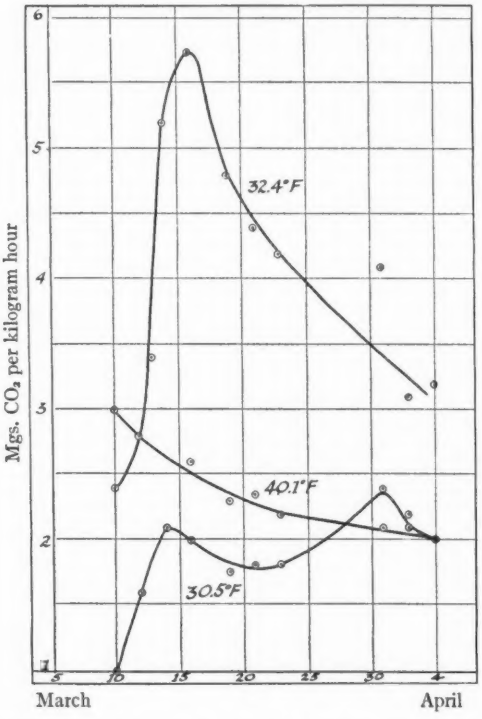

FIG. 4.—Respiration of tubers of Russett Rural potatoes at 30.5°, 32.4°, and 40.1° F., plotted against time.

centration and the respiration, which might throw some light on the mechanism by which the oxidation process is accelerated at 0° C.

METHODS OF ANALYSIS

In connection with respiration (experiment III), analyses were made of the total and reducing sugars of other tubers from the

same lot as used in the cold storage rooms, and samples were taken at certain intervals.

Sampling.—About six or eight tubers were selected, and after they were washed, several cylindrical plugs were cut from each. The cylinders were then put through a sampling machine, which reduced the tissue to a very fine pulp. The pulp was thoroughly mixed.

Moisture.—Samples were rapidly weighed in glass weighing bottles for moisture determinations, and covered with alcohol to prevent oxidation. Most of the alcohol and water was evaporated on a water bath, and then the specimens were dried to a constant weight in a vacuum over phosphorus pentoxide.

Sugar.—Fifty gm. of the pulp was weighed out to the nearest centigram, and covered with about an equal amount of 50 per cent alcohol. After extracting, making up to volume, evaporating the alcohol from an aliquot, clearing with lead acetate, and removing the excess of lead, the reducing sugars were determined gravimetrically according to the MUNSON and WALKER (**9**) method. After inversion with HCl in the cold for twenty-four hours, the total sugars were determined by the same method.

Hydrogen-ion concentration.—The rest of the pulp was thrown on a filter, and the filtrate allowed to drip into a beaker which was placed in a boiling water bath. This stopped the oxidase action, and also caused the filtrate to separate into a thick curd and a clear liquid. Colorimetric hydrogen-ion concentration determinations were then made on the latter, using GILLISPIE'S (**6**) method.

RESULTS

EXPERIMENT I.—The figures for moisture are in each case the average of duplicate determinations. The results are shown in tables V, VI, and VII.

TABLE V

CARBOHYDRATE CHANGES AT 0.22° C. (32.4° F.)

Determination	3/13/23	3/15	3/17	3/19	3/21	3/23	3/28	4/6	4/14	4/18	4/26
Moisture	76.45	80.28	78.34	75.86	79.40	79.00	79.48	78.94	77.27	.....	79.74
Pn	6.1	5.7	6.1	6.0	6.1	6.3	6.1	.....	.....	.....	.....
Reducing sugar percentage	0.660	0.778	0.778	0.814	0.884	1.445	1.556	1.65	2.42	1.88	2.09
Total sugar percentage	1.044	1.006	1.192	1.194	1.420	1.726	1.938	2.38	2.91	3.33	3.38
Sucrose percentage	0.365	0.216	0.459	0.361	0.509	0.267	0.353	0.366	0.465	0.427	0.272

Both the reducing and total sugar percentages are calculated on the wet basis, and expressed as percentage of invert sugar. The percentage of sucrose is obtained by multiplying the difference between the total and reducing sugar by the factor 0.9. Correction was not made for the volume of alcohol precipitate. Because of lack of time starch analyses were not made.

With one or two exceptions, the determinations of the hydrogen ion concentration in all cases are constant, within the limit of error

TABLE VI

CARBOHYDRATE CHANGES AT −0.83° C. (30.5° F.) AND 1.17° C. (34.1° F.)

Determinations	−0.83° C. (30.5° F.)						1.17° C. (34.1° F.)		
	3/19/23	3/22	3/24	3/29	4/2	4/26	3/19/23	3/23	3/29
Moisture	77.73	78.42	78.12	79.39	80.00	79.82	79.68	75.92	76.75
P_H	6.0	6.1	5.7	6.1	.....	.....	5.9	6.0	6.0
Reducing sugars percentage	0.638	0.660	0.710	0.486	0.158	1.83	0.828	1.112	1.244
Total sugar percentage	0.832	0.760	0.890	0.894	0.992	3.53	1.066	1.504	1.704
Sucrose percentage	0.184	0.101	0.171	0.388	0.792	1.61	0.266	0.372	0.437

TABLE VII

CARBOHYDRATE CHANGES AT 4.5° C. (40.1° F.)

Determinations	3/22/23	3/28	4/3	4/9	4/14	4/18	4/26
Moisture	78.04	76.36	.....	81.69	78.72	78.87	79.97
P_H	6.0	6.0	.....	.....	.....	.....	.....
Reducing sugar percentage	0.562	.....	0.604	0.634	0.664	0.332	0.468
Total sugar percentage	0.760	.....	0.674	0.756	0.768	0.652	0.650
Sucrose percentage	0.188	.....	0.066	0.116	0.099	0.304	0.173

of the colorimetric method, at P_H. 6.0–6.1, and therefore this does not appear to be a factor concerned in the physiological changes observed.

The moisture content, while somewhat irregular, does not appear to vary in any particular manner. As regards reducing sugar (fig. 5), it is seen at 0.22° C. (32.4° F.) to increase slowly at first, and then rise rapidly during the thirteenth to fifteenth day of storage, after which it again increases slowly. At −0.83° C. (30.5° F.) the peculiar fact is noted that after rising to a slight maximum the percentage of reducing sugars actually decreases. At 1.17° C. (34.1° F.) for the three analyses made there is a considerable increase

in reducing sugar, while at 4.5° C. (40.1° F.) the amount is almost constant throughout, showing an increase of only 0.1 per cent in period between the first and last analysis. In almost all cases the 3 total sugars (fig. 6) parallel the reducing sugars, and are greater, showing little changes, therefore, in the sucrose content. The

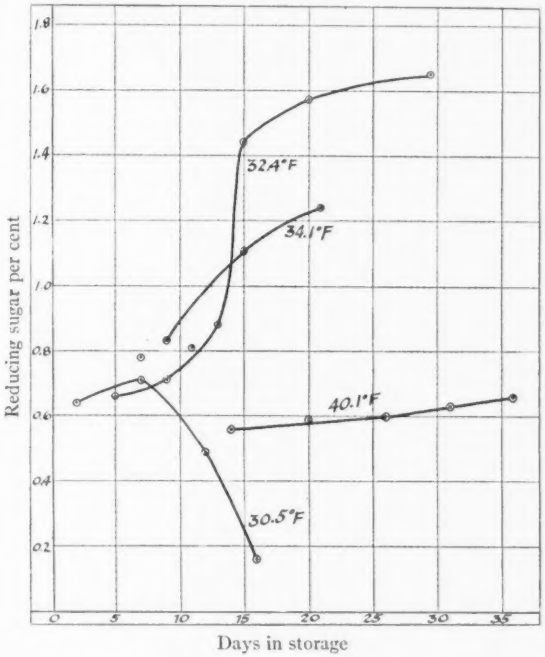

FIG. 5.—Variation in amount of reducing sugar in tubers of Russett Rural potatoes held at low temperatures.

exception to this is −0.83° C. (30.5° F.), where the total sugars gradually increase while the reducing sugars decrease. This may indicate that sucrose is increasing at the expense of invert sugar.

EXPERIMENT II.—This was performed to determine the effect of temperature change on carbohydrate transformations in the tubers used in experiment I. Tubers which had been held at 0.22° C. (32.4° F.) were moved to 4.5° C. (40.1° F.), and others

which had been held at 4.5° C. were moved to 0° C. Table VIII shows the effect on reducing and total sugar. Considerable increase

TABLE VIII

EFFECT OF CHANGING TEMPERATURE ON CARBOHYDRATE TRANSFORMATION IN TUBERS

Date	Moved from 4.5° C. (40.1° F.) to 0° C. (32° F.)			Date	Moved from 0.22° C. (32.4° F.) to 4.5° C. (40.1° F.)		
	Reducing sugar percentage	Total sugar percentage	Sucrose percentage		Reducing sugar percentage	Total sugar percentage	Sucrose percentage
4/7.....	0.572	0.816	0.231	4/10.....	2.540	2.988	0.426
4/9.....	0.688	0.806	0.112	4/13.....	2.486	2.786	0.285
4/14.....	0.360	0.512	0.114	4/18.....	2.292	2.954	0.629
4/18.....	0.618	1.150	0.486	4/21.....	2.136	2.910	0.735
4/26.....	0.974	1.578	0.574	4/26.....	1.722	2.292	0.541

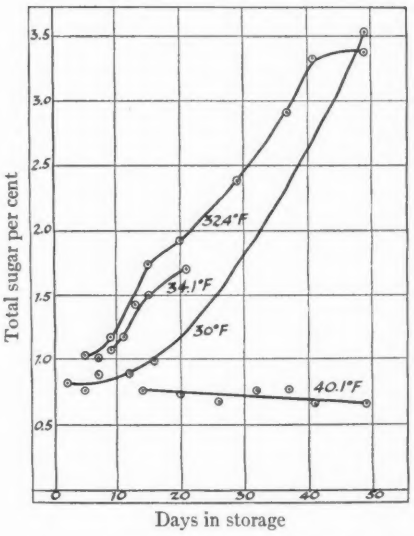

FIG. 6.—Variation in amount of total sugar in tubers of Russett Rural potatoes held at low temperatures.

in total and reducing sugar is noted in the 4.5° C. (40.1° F.) to 0° C. (32° F.) test, and a like decrease in the other (fig. 7). The latter result is in agreement with results reported in the literature on the starch-sugar equilibrium.

Discussion

From the results reported in this paper it appears that the temperature-respiration curve in the case of potato tubers does not consistently decline as the temperature decreases, but declines to a low point at about 3.0° C. (37.4° F.), increases at 0° C. (32° F.), and again declines. This increase in respiration the writer believes is due to an accelerating effect which takes place in some

manner at or near 0° C. (32° F), which causes the respiratory activity to be abnormally high for some time.

At the time the respiration at 0° C. (32° F.) is passing through a maximum, there is a gradual accumulation of both reducing and total sugar, and when the respiration begins to decline the sugar is increasing rapidly. PALLADIN and KOMLEFF (**13**) have shown that the concentration of sugar in the nutrient solution in which etiolated bean seedlings were placed affects their respiration markedly, and, as before mentioned, BUTLER interprets the data of MÜLLER-THURGAU as showing that respiration in potato tubers is more influenced by the sugar concentration than by temperature. If we postulate further that there is an optimum concentration of sugar for enzyme production or action and that higher concentrations inhibit, we can explain the rise as well as the fall in the respiration rate, and also the decrease of diastatic action. This is offered as a tentative explanation. It is possible that, as suggested by SPOEHR and MCGEE (**15**), increases in the amino acid content may have been responsible for the increase in the respiratory activity, but it also seems significant that the latter was accompanied by certain changes in sugar concentrations. In connection with the rest period in potatoes, such a respiratory stimulus would explain the results of MÜLLER-THURGAU (**11**) in breaking the rest period by holding at low temperatures, providing we accept APPLEMAN'S (**2**) view that the shortening of the rest period is brought about by conditions which accelerate respiration.

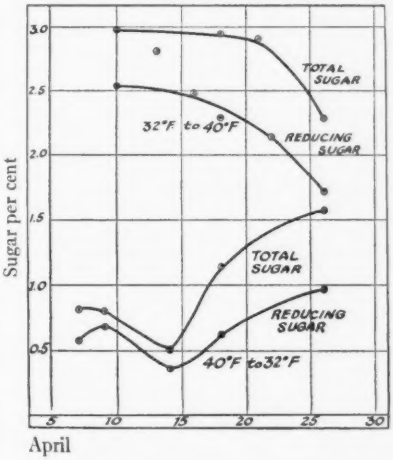

FIG 7.—Effect on sugar-starch equilibrium of moving potato tubers stored for some time at 32° F. and 40° F. to 40° F. and 32° F. respectively.

Summary

1. In determining the respiration of potatoes at low temperatures, there was found to be a marked acceleration in the rate at 0° C. (32° F.), such that for a considerable period the intensity was greater than at 4.5° C. (40° F.). This stimulation passed through a maximum and then decreased, but at the end of the experiment was still greater than 4.5° C.

2. The curve of respiration for temperatures from −0.83° C. (30.5° F.) to 11.5° C. (52.7° F.) was determined. A minimum point in this curve was found to be at about 3.0° C. (37.4° F.), and as the temperature decreases respiration increased at 0.° C (32° F.), and again declined.

3. The carbohydrate changes were studied at various temperatures, and it was found that sugar accumulation at 0° C. (32° F.) is slow at first, then increases rapidly, and finally decreases. At 4.5° C. (40° F.) the sugar content is nearly constant, at 1.17° C. (34° F.) it increases fairly rapidly from the start, while at −0.83° C. (30.5° F.) there is gradual increase in total sugars but a decrease in reducing sugar.

4. In agreement with results reported in the literature, it is found that sugar accumulated in potatoes at 0° C. (32° F.) began to disappear rapidly when they were stored at 4.5° C. (40° F.).

5. It is suggested that the acceleration of respiration at 0° C. (32° F.) is dependent on the changing concentration of sugar, and that up to a certain concentration sugar increases respiration, and beyond that inhibits it.

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A STUDY IN THE GROUPING OF PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 326

HILARY STANISLAUS JURICA

(WITH FOURTEEN FIGURES)

Botanists are often impressed with the rather striking fact that frequently not only mere clumps, clusters, or groups of a given species are seen on a field trip, but at times considerable patches or even entire areas seem to be dominated by a single species. What are the factors responsible for this grouping, especially in the case of a virgin prairie? It is certainly not a felicitous scattering of seeds, for the plants are seldom annuals, and but few perennials would survive the struggle to get a foothold. At least in this case, animals, winds, or water cannot be considered as possible agencies. It is with a view to interpret this grouping that this investigation has been entered upon.

Some attention has been paid to this line of work by previous workers, notably IRMISCH, SACHS, HEGEMAIER, and HOLM, and recently the subterranean organs of some of our pernicious weeds have been studied by PAMMEL and HITCHCOCK, not so much from a morphological or ecological viewpoint, but as to the means of their eradication.

On the basis of vegetative propagation, perennials have been divided into crown-formers, those that propagate by rhizomes, and those that propagate by means of adventitious buds upon creeping roots. According to HITCHCOCK (1), crown-formers are perennial plants which have no well marked adaptation for vegetative propagation, but in which the base of the stem or stems live throughout the winter, and new shoots are produced from buds upon the base of these stems. In some plants the crown is short and compact upon a well marked taproot, as in *Taraxacum*. The present investigation, however, does not cover crown-formers, but deals with both creeping horizontal and vertical rhizomes.

Horizontal rhizome

In the case of *Polygonatum multiflorum*, as described by SACHS (4), "the new lateral shoot arises each year in the axil of the ninth and last scale leaf, and the succeeding leaves are foliage leaves on slender elongated internodes, while the internodes on the basal portion between the membranous scale leaves are thick and short. The leaves are in two rows on the basal parts, alternately right and left, as may be seen by their scars."

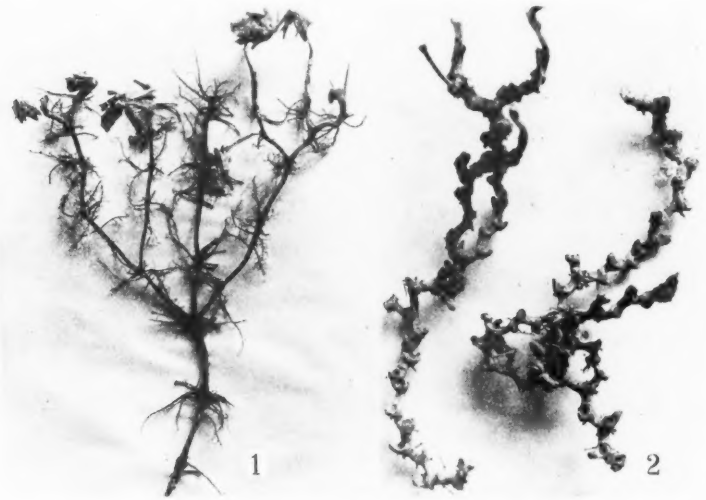
In his work on *Podophyllum peltatum*, HOLM (2) reports a similar regularity, except that at times variations occur; the bud which develops in the axil of the definite scale leaf frequently remains dormant, and another bud from another scale leaf grows out as a long horizontal shoot, continuing the direction of the rhizome. HOLM also reports that bifurcation in *P. peltatum* is not uncommon, depending upon the non-development of the regular large bud, "which is then replaced by two other buds in the axils of other scale leaves, both of which are then situated to the right and left of the axis." These two buds then develop simultaneously into two horizontal shoots with elongated internodes, only to repeat the process of producing new buds annually and new bifurcation occasionally.

To what extent is this continued, and what relation do the individual plants making up the large almost circular patch of *P. peltatum* bear to each other? HOLM, who also studied the germination of this plant, answers this in part, for he found that the fruit falls without bursting, and the seeds which are closely imbedded in the gelatinous pulp naturally germinate and grow in small clumps, flowering only after four or five years of growth. This of course accounts for the almost circular nature of the dense patches so frequently found in the woods. The extension and enlargement of the patch then depend mainly on the vegetative propagation described by HOLM, but its density in number depends upon the additional germination of new clumps within.

The writer has carefully dug up portions of a number of patches, and found that, just as regularly as the plant is proceeding in a given direction by the anterior growth and prolongation of the horizontal subterranean stem year by year, so also the horizontal rhizome is gradually and regularly subject to decay at the posterior end.

When this decay reaches a bifurcation of a probably much branched rhizome, a breaking up of this complex plant into simpler or apparently single plants is the result.

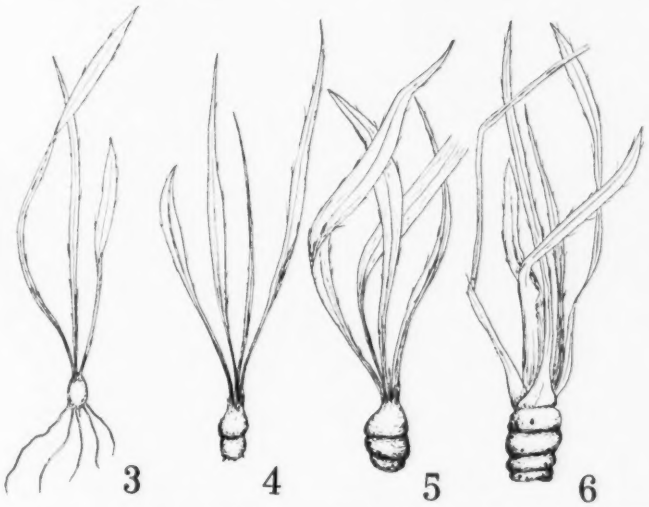
Fig. 1 shows the extensive branching of this plant, as well as its regular elongation. A counting of the scars along any one branch to the end of the main stem shows little more than seven years of growth. This is the greatest extent of time which the extensive digging revealed, due no doubt to ceasing of function and subse-



FIGS. 1, 2.—Fig. 1, branching horizontally creeping rhizome of *Podophyllum peltatum*, showing last seven years of growth and number of shoots arising therefrom; fig. 2, branched rhizome of *Smilax herbacea*, showing scars of over thirty years of growth.

quent death and decay of the posterior region. Fig. 1 also shows that this plant bears seven new shoots, and probably would have borne more if one of the branches had not been subject to mechanical injury. This means that often plants of *P. peltatum*, which from a surface view appear to be single, are in reality joined together by a common creeping rhizome. This, together with the failure of the fruit to burst and the subsequent germination of its seeds in small clumps, is responsible for the dense patches dominating an almost circular area.

That this vegetative propagation (or a modification of it) is true of many other plants with creeping rhizomes, and hence an indication of the probable cause of the dominance of a given area by a given species of a perennial, is evident from a study of *Smilax herbacea* (fig. 2), which shows the same regularity already described in producing elongated shoots in axils of definite scale leaves, the shoots alternating right and left. Unfortunately, this rhizome was damaged and parted in being dug up, but nevertheless it shows that five of the plants appearing as single are in reality produced by a



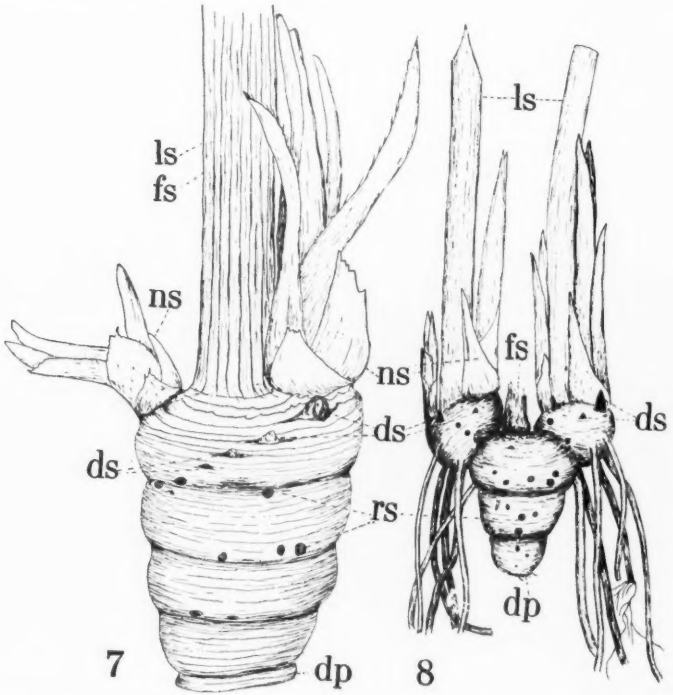
FIGS. 3–6.—*Eryngium yuccifolium;* vertical rhizome of one, two, three, and four years of growth respectively.

single branched rhizome. The woody nature of the rhizome of *S. herbacea* of course resists posterior decay more readily, hence over thirty years of growth are easily accounted for.

Vertical rhizome

What is true of plants with horizontal stems is likewise true of plants with vertical rhizomes, of course with modifications. A good example is *Eryngium yuccifolium.* The germination studies in this genus have been made by MOEBIUS (3) in his investigation upon the

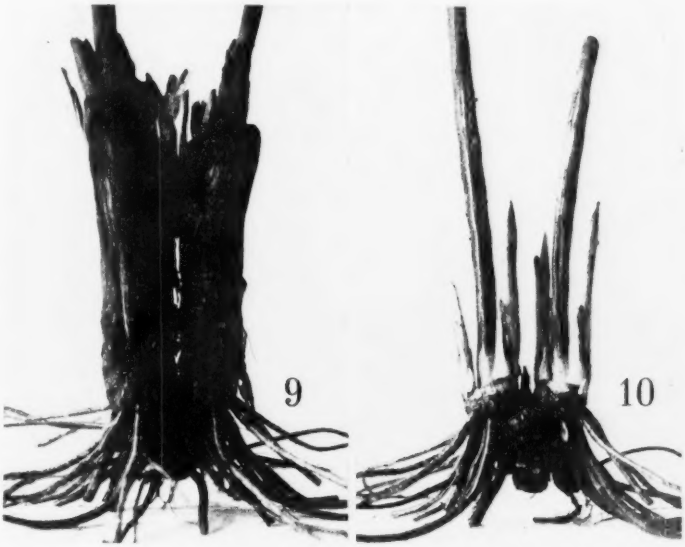
apparently monocotyledon-like nature of *Eryngium*. Unfortunately, however, MOEBIUS did not include a study of the rhizome. I found that *E. yuccifolium* does not flower until the fourth, more commonly the fifth year (figs. 3–7).



FIGS. 7, 8.—Fig. 7, *Eryngium yuccifolium:* vertical rhizome, showing five years of growth, first flowering stem, new shoots arising from axils of uppermost basal leaves, and dormant buds or shoots in axils of some other basal leaves; fig. 8, older branching rhizome; *rs*, root scars; *ds*, dormant shoot or bud; *ns*, new shoot; *ls*, last flowering shoot; *dp*, decaying posterior end of rhizome; *fs*, first flowering shoot.

Its growth is limited for the first four years, for it sends forth annually a circle of but four to seven leaves (figs. 3–6), whereas an adult flowering plant develops a circle of fifteen and sometimes even of twenty-one leaves; of course, some of these are then borne on the flowering stem. The food manufactured by the leaves for

the first four years serves to develop a strong vertical rhizome (figs. 3–7). After flowering the fifth year, as well as all subsequent years, the erect flowering stem dies, leaving a scar on the crown of the vertical rhizome. Before winter has set in, which naturally destroys the leaves and stem above the ground, a bud is produced in the axil of each of the five or six basal leaves arising from the vertical subterranean rhizome (figs. 7, 8). Only two of these buds develop



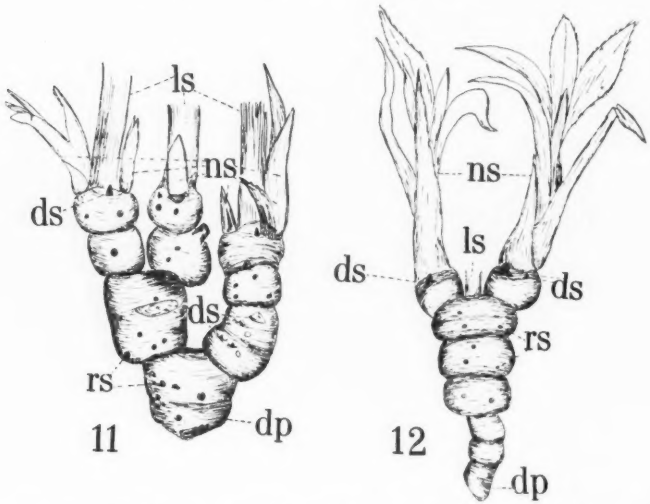
FIGS. 9, 10.—Fig. 9, *Eryngium yuccifolium:* rhizome dug up in midwinter (January 19), showing dead basal leaves protecting developing new shoots; fig. 10, basal leaves removed.

into flowering shoots; the rest abort. I have found, however, that whenever any of the ordinarily developing buds (that is the innermost and uppermost) are injured or destroyed, one of the dormant or aborted buds develops in its place. Keeping the rhizome in water for a time has also caused some of the aborted buds to begin to develop flowering stems.

As already stated, the top of the leaves above the ground freeze and dry up, but they still remain attached to the rhizome under-

ground, serving to protect the developing buds arising in their axils. Fig. 9 shows a compound plant dug up on January 19, 1921, with the old leaves attached, and fig. 10 is the same with the leaves removed. Some of the roots have been cut away so as to expose the desired feature. One can easily note the scars and old flowering stems as well as the developing buds.

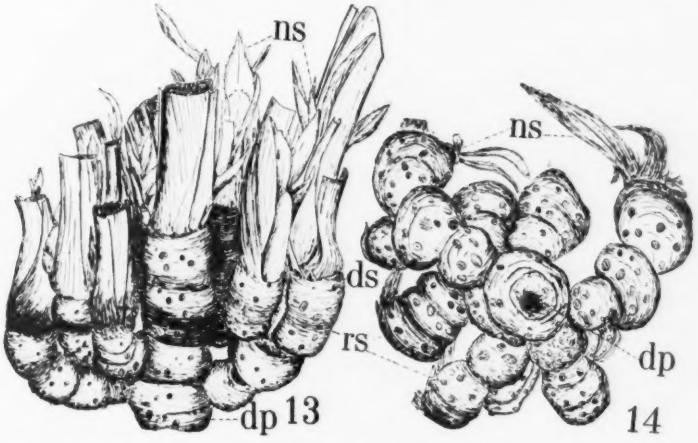
The principal feature in this study, however, is the regularity with which *E. yuccifolium* produces flowering stems, the definite



FIGS. 11, 12.—Fig. 11, *Eryngium yuccifolium:* irregular lateral branching of vertical rhizome; fig. 12, individual plant separated from group by decay of rhizome reaching region of branching.

law which it follows. It flowers the fourth or fifth year, produces five or six buds in the axils of its basal leaves, and develops two of these into flowering stems the sixth year (fig. 7). In turn these again develop buds in the axils of the basal leaves, so that after repeated years quite a group of united plants is produced (figs. 13, 14). At times one of the lateral buds fails to develop, which of course results in irregular branching (fig. 11). One could easily and fairly accurately estimate the age of any cluster of *E. yuccifolium*, were it not for the fact that unfortunately, just as in the

case of horizontal stem, decay starts in the older lower or posterior part. That is, the plant is gradually developing anteriorly, but at the same time decaying posteriorly. Whenever the decay reaches the crown of a rhizome connecting branching, superimposed



FIGS. 13, 14.—*Eryngium yuccifolium:* lateral and bottom view of much branched rhizome.

rhizomes, partition and breaking up into individual plants take place (fig. 12). To what extent this branching and subsequent grouping are possible is evident from figs. 13 and 14; hence, it is vegetative propagation which is mainly responsible for the dominance which certain species hold in given areas.

Summary

1. Many plants reproducing vegetatively spend a number of years in developing either a horizontal or vertical rhizome, before sending forth a flowering stem.

2. Both horizontal and vertical rhizomes grow at the anterior end, and die and gradually decay at the posterior end.

3. Horizontal and vertical rhizomes branch mostly by means of bifurcation.

4. New shoots arise with great regularity from the axils of certain leaves.

5. Although buds arise in the axils of a number of the leaves, but one or two develop, the rest abort or remain dormant.

6. When a regular developing shoot is destroyed, one or more of the dormant buds develop in its place.

7. Placing a rhizome of *Eryngium yuccifolium* in water causes some of the dormant buds to develop.

8. Plants reproducing vegetatively are able to invade and dominate already overgrown areas.

9. Vegetative reproduction is generally responsible for both the close grouping of many plants and their dominance in a given area.

10. The flowering shoots arising from the branches of the subterranean rhizome, viewed from the surface, give an impression of many individual plants, whereas in reality they are connected by a common rhizome.

11. When the gradual decay of the posterior end of a creeping horizontal or of a superimposed vertical branched rhizome reaches the region of branching, a breaking up of the group into non-connected individual plants takes place.

Acknowledgment is due to Professors CHARLES J. CHAMBERLAIN and HENRY C. COWLES for suggestions and criticisms.

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MEIOTIC CYTOKINESIS OF CANNABIS[1]

HUGH C. MCPHEE

(WITH PLATE VII)

During the summer of 1922, the writer investigated the meiotic divisions in the pollen mother cells of *Cannabis sativa*, for the purpose of throwing some light upon the cause of the variability of pollen grain size which occurs in this species. Although the results obtained were not conclusive, so far as the solution of the problems at hand were concerned, it seems desirable to publish a short account of meiosis in this plant, and to add another to the several already reported cases of cytokinesis by furrowing in the cells of higher plants. Since an excellent review of the literature dealing with this interesting phase of plant cytology has been given by FARR (2), it does not seem necessary to take space for literature review here.

STRASBURGER (6) published a few figures of meiotic divisions in *Cannabis*, mostly of the anaphase of the heterotypic division, showing ten chromosomes as the reduced number. In the root tips of the staminate and of the pistillate plants, he found that the chromosomes apparently were identical in size and shape, and no indication of a sex chromosome was observed. The results of recent research, however, have shown that so many irregularities occur in the development of the staminate buds, that a more complete account of chromosome behavior during the reduction division in this plant is desirable. The series of drawings in pl. VII show the changes which take place from the time of the archesporial cell to the liberation of the pollen grains.

Materials and methods

The material for this study consisted of staminate buds fixed whole in ALLEN'S (1) modification of Bouin's fluid. This reagent was found to be very satisfactory for fixing and preserving both the chromatic and the achromatic figures, although there is a slight tendency to cause shrinkage of the tissue. Considerable time and

[1] Contribution from Bussey Institution of Harvard University.

labor were saved by examining one anther from a bud while in the fresh condition, after staining and fixing with aceto-carmine. If the material proved to be in the right stage for study, the remainder of the bud was fixed at once. It was found that the best time to collect buds for studying the reduction division was between 7:00 A.M. and 11:30 A.M. Attempts to obtain satisfactory material in the late afternoon were practically without success.

The examination of large numbers of cells is facilitated by the fact that in a longitudinal section of a staminate bud many pollen mother cells are to be seen within a single loculus. In the premeiotic conditions the archesporial cells are crowded closely together, and occupy the whole space inclosed by the lining of tapetal cells. The greater part of each cell is filled with a rather dense cytoplasm, homogeneous in appearance. In the center or slightly to one side can be seen the large, nearly spherical nucleus, with a well defined membrane, and containing the deeply stained nucleolus. During the premeiotic period the chromatin is in such a fine state of division that no definite units can be observed, and it is not until the formation of chromatin threads during the early stages of synapsis that definite chromatin elements become visible.

The tapetal cells are conspicuous during all stages of meiosis as a ring of closely packed cells, lining the loculus of the anther. During the early synapsis stages of the mother cells, the nuclei of the tapetal cells divide mitotically, but the cells do not divide. These binucleate cells then remain in this condition until the rupture of the mother cell wall, when they begin to disintegrate and soon disappear.

Heterotypic division

The first indication of preparation for the heterotypic division is a slight enlargement of the nucleus and the appearance of a fine network pervading the space inclosed by the nuclear membrane. This fine mesh of threadlike elements appears to extend in all directions in a criss-cross manner, completely filling the nucleus and usually enveloping the nucleolus; but the threads are so fine and cross each other so frequently that it is impossible to make accurate counts of the number present. The next step is a gradual contraction of the chromatin material away from the nuclear membrane.

The condensation is not uniform at all points, and frequently the intertwining mass is found at one side of the nuclear cavity (fig. 4). The continued withdrawal from the periphery of the nuclear cavity causes the individual elements to become very closely massed together. The nucleolus at this time is usually found surrounded by chromatin, although cases have been observed where it was almost free and lay between the chromatin complex and the nuclear membrane. That this period of the nuclear reticulum and chromatin contraction is a relatively long one, is indicated by the fact that much of the material examined was in this stage of development, and seldom did the mother cells at the opposite ends of a loculus show appreciable differences. In some of the later stages, where development is more rapid, it is possible to observe synapsis stages in one end of the loculus and mother cells with two nuclei in the opposite end.

The relatively long period of contraction which passes under the name of synapsis is one during which the chromatin threads are in such close association with one another that little can be learned from observing the closely contracted mass. Fig. 5 shows the appearance of a typical cell at this time. When the chromatin complex begins to expand, the threads spread out in all directions until they reach the limiting membrane. As the threads emerge from the synaptic knot they are thicker, fewer in number, and more twisted about one another than in the early prophase. As the threads reach the membrane they contract more and more, until short, rod-shaped chromosomes are formed. The paired chromosomes which result from this contraction are shown in the region of the nuclear membrane in fig. 8.

From the end of the synaptic period, when the chromosomes are found in the region of the nuclear membrane, to the time when they are arranged in the center of the cell preparatory to being pulled apart to the opposite poles, is a period of many and rapid changes in the cell. The nucleolus, which up to this time has been very conspicuous, begins to fade and finally disappears. At about the same time the nuclear membrane very suddenly disappears. The chromosomes migrate to the center of the cell, the spindle fibers radiate into this mass from the poles of the bipolar cell, and the

chromatin units again become indeterminate. The daughter chromosomes remain in this position only a short time before they begin to move apart to the opposite poles of the cell. A polar view of the chromosomes just after they have left the plate shows them well separated and ten in number. The unusual tangential view shown in fig. 12 shows the whole twenty chromosomes as they are leaving the plate, and gives a good demonstration of their morphological identity. As the two groups of daughter chromosomes approach the opposite poles of the cell each begins to contract, and passes through a series of obscure changes, the net result of which is the formation of a complete nucleus. The heterotypic division is now complete, and the binucleate cell awaits the beginning of the homotypic division, which starts almost immediately.

Homotypic division

The homotypic division is characterized by greater rapidity than the heterotypic division, and therefore is less easily observed. At the beginning of this period the chromatin is usually found in a very fine state of division, although it is not uncommon to see small pieces of chromatin which have not undergone complete transformation in the region of the nuclear membrane. The general course of events is much the same as in the heterotypic division, but from the interkinesis condition shown in fig. 14 to the formation of the spindles is an exceedingly obscure period. The threadlike elements of each nucleus contract to form masses of chromosomes, which become arranged in the center of the nuclear cavity; the nuclear membranes and the nucleoli disappear, and spindle fibers appear. The details of these events are difficult to observe. There seems to be much less separation of the chromatin elements during this division than during the heterotypic, and as a result it is practically impossible to follow individual chromosomes. Sometimes both nuclei divide at about the same time, but in other cases one nucleus may be seen in the telophase when the other is just starting to form the mitotic figure. The divisions may both occur in the same plane, or at right angles to each other, or in various planes at different angles to one another. Fig. 15 shows both division figures parallel and in the same plane. The usual result of such an oc-

currence is that all four nuclei can be seen in one section of the mother cell, a rather unusual condition in *Cannabis*. The most usual condition is to see three of the four nuclei (fig. 17). As the chromosomes leave the equatorial plate in the homotypic division they are much massed together, and only in exceptional preparations can the chromosome number be determined. The final stages which follow are much the same as in the heterotypic division; the four chromosome groups become rounded off, a membrane forms about each, the spindle fibers disappear, and there results a cell with four nuclei. The cytoplasm is homogeneous in appearance throughout the cell, no connecting fibers are to be seen between the nuclei, and traces of a cell plate are entirely absent. The condition of the mother cell at this stage is represented in fig. 17.

Cytokinesis

After the meiotic divisions have been completed there is a relatively long period of apparent inactivity within the mother cell. Sections of whole buds frequently show all of the mother cells in this condition, with no indications of further development. The first sign of further change is the appearance of constrictions in the cytoplasm, at four points on the periphery, but inside the mother cell wall and at equal distances from the nuclei. The first visible effect of these constrictions, as seen in a section of the cell, is a change from the nearly spherical to a triangular form. The constrictions become very sharp and extend to the center of the mother cell, cutting it into four parts. Many mother cells can be found which show the completed process, but due to its extreme rapidity, cells which show the constrictions only part way to the center are more rare (fig. 19). The writer has observed a similar process in the mother cells of *Nicotiana*, where it is much less rapid in its development and correspondingly easier to follow.

Until recent years the method of cytokinesis in the dicotyledonous plants was supposed to be by the formation of a cell plate, and this feature was one which constituted a distinction between plant and animal cells. FARR (**2, 3**), however, has shown that cytokinesis by furrowing occurs in the dicotyledons *Nicotiana*, *Primula*, *Helianthus*, *Ambrosia*, *Tropaeolum*, *Chrysanthemum*, *Magnolia*, and

in the monocotyledons *Sisyrinchium* and *Nelumbo*. Mrs. W. K. FARR (4) has found the same process in *Cobaea*. GATES and REES (5) reported a similar process occurring in the pollen mother cells of *Lactuca*. It is evident, therefore, that the occurrence of cytokinesis by furrowing is not as rare among plants as it was thought to be a few years ago, and it is probable that more examples will be found as more plants are investigated. FARR (3) reports that the division of the mother cells in *Nelumbo* is accomplished in part by furrowing and in part by the formation of a cell plate. A cell plate starts to form at the periphery of the cell, and after extending in for a short distance disappears. The process is then completed by the formation of furrows which divide the cell into four parts.

After the formation of the pollen grains as a result of the rapid extension of the furrows to the center of the mother cell, each grows somewhat and rounds off, although the shape of the pollen grains is never exactly spherical while they are retained within the mother cell wall. Finally, the wall of the mother cell is ruptured, the pollen grains pass through a period of growth and assume a spherical form, filling the loculus and awaiting the dehiscence of the anther.

Summary

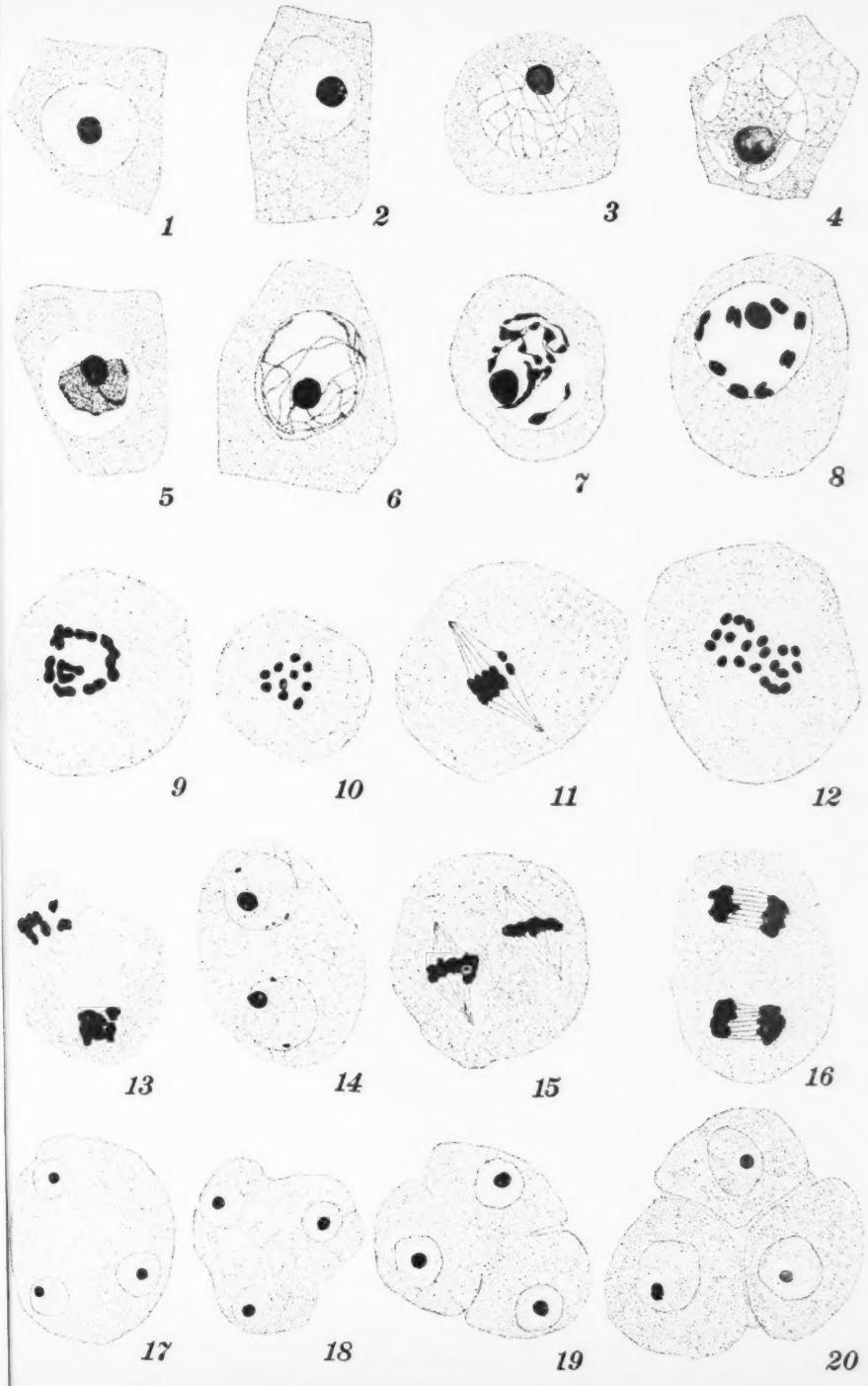
1. Counts made in the pollen mother cells of *Cannabis sativa* show that the reduced number of chromosomes in this species is ten.

2. The reduction division commonly occurs during the period from sunrise to noon. Although mitotic figures can be found in material collected during the afternoon or evening, they are comparatively rare.

3. The heterotypic division is easily studied, and chromosome counts are most easily made during the anaphase of this division. The behavior of the chromosomes is normal, and no unusual features were noted.

4. Little can be learned concerning the individual chromosomes during the homotypic division, because of the massing of cell elements and the rapidity of the division.

5. There is no morphological evidence that any one of the ten chromosomes is a sex chromosome.



McPHEE on CANNABIS

6. The method of cytokinesis is by furrowing. The furrows appear at the periphery of the cytoplasm and at points equidistant from the mother cell nuclei. These furrows extend rapidly to the center of the mother cell, cutting it into four parts.

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EXPLANATION OF PLATE VII

All drawings were made with the aid of a camera lucida, and all figures were drawn from single sections; magnification 1800 diameters.

FIG. 1.—Archesporial cell.
FIG. 2.—Archesporial cell showing shrinkage of cytoplasm.
FIG. 3.—Parasynapsis.
FIG. 4.—Contraction of chromatin.
FIG. 5.—Synizesis.
FIG. 6.—"Open spireme" showing conjugation of threads.
FIG. 7.—Condensation of threads to form chromosomes.
FIG. 8.—Diakinesis.
FIG. 9.—Metaphase of heterotypic division, polar view.
FIG. 10.—Anaphase, polar view, showing ten chromosomes.
FIG. 11.—Metaphase, side view.
FIG. 12.—Tangential view, late metaphase.
FIG. 13.—Daughter chromosomes at poles.
FIG. 14.—Interkinesis, nuclei in resting condition.
FIG. 15.—Metaphase of homotypic division, side view.
FIG. 16.—Anaphase of homotypic division, side view.
FIG. 17.—Mother cell showing three resting nuclei.
FIG. 18.—Mother cell showing beginning of furrowing.
FIG. 19.—Constrictions extending to center of cell.
FIG. 20.—Four pollen grains before rupture of mother cell wall; mother cell wall not shown.

A SPARGANIUM FROM THE MIDDLE EOCENE OF WYOMING

EDWARD W. BERRY

(WITH SEVEN FIGURES)

In studying a collection of fossil plants from the Wind River basin, of Middle Eocene age, made by Mr. N. H. BROWN of Lander, Wyoming, I have found, among other interesting forms that shed much light on the environment of the mammalian fauna known from this horizon, a series of specimens that so admirably illustrate the methods of paleobotany in dealing with fossil plant remains preserved as impressions, that they seemed to me to merit special comment.

Paleobotanists are often criticized by botanists, who insist on the futility of attempting to determine species from the foliage alone. In this connection attention is called to the fact that in general foliar organs are more conservative than either vascular, floral, or carpological structures.

In dealing with impressions of plants it often becomes necessary to describe detached objects of various kinds. Most often these are leaves, but at times are stems, fruits, flowers, and various other detached parts. Often their botanical relations are only partially understood, or they may even be entirely misunderstood. It is desirable to have such objects described and figured, however, not only because they may be of great chronological value to the geologist, but also because they are frequently of importance in the attempt to determine past environments.

It is quite possible to get a considerable knowledge of such an environment from a representative collection of fossil leaves, even though all of them are wrongly identified or even remain undetermined. This is also justified from a purely botanical point of view, since sooner or later someone with better material will obtain the clue to their true botanical position, or will be able to correlate the scattered parts into a complete and convincing whole, as I

believe that I have done for the species of *Sparganium* which is the subject of this note.

In 1882 NEWBERRY[1] described some objects from the Green River beds of Wyoming which he called *Brasenia*(?) *antiqua*. It should be noted that these objects are entirely different from the Canadian *Brasenia antiqua* of DAWSON, which latter have since been referred to *Nelumbo*. The Middle Eocene remains that NEWBERRY thought represented an extinct species of *Brasenia* consisted of branched stems bearing spheroidal fruit heads, made up of individuals which he described as small club-shaped pods, although he states that the specimens were too imperfectly preserved to permit any decisiveness in their identification. No additional material similar to that studied by NEWBERRY, which is preserved in the National Museum (no. 7018), has been collected from the Green River beds.

In 1923 KNOWLTON[2] published a revision of the flora of the Green River formation, describing certain leaves under the name of *Pontederites hesperia*, and these he compared with those of the existing pickerel weed, *Pontederia*. He believed that these leaves represented some Eocene member of Pontederiaceae. They lacked their basal portions, but were of considerable size, with mostly parallel longitudinal veins connected by transverse veinlets.

The Wind River material which furnished the collections for this study was contained in beds which have a high content of volcanic ash, and were for the most part water-laid, that is, they are tuffs. The surfaces of some of the slabs are covered with numerous fruit heads, dissociated fruits, and stem fragments which are identical with those from the Green River beds that NEWBERRY called *Brasenia*(?) *antiqua*. In several instances these fruit heads are attached to the branches upon which they were borne in life. These heads are of various sizes, ranging from 5 to 12 mm. in diameter, and are made up of numerous small symmetrical beaked fruits, arranged radially on a spherical central receptacle. In some cases these tiny fruits have been replaced by silica, and hence show their

[1] NEWBERRY, J. S., U.S. Nat. Mus. Proc. **5**:514. 1882; U.S. Geol. Survey Mon. **35**:93. *pl. 68. fig. 7.* 1898.

[2] KNOWLTON, F. H., U.S. Geol. Survey Prof. Paper **131**:154. *pl. 36. fig. 6.* 1923.

general form with great fidelity. They are round and approximately symmetrical in cross-section, about four times as long as their maximum diameter, narrowed like the neck of a waterbottle above the middle, and slightly expanded at their distal end. Their surface is smooth, and they show no structural details. Those that are partly eroded are seen to be hollow.

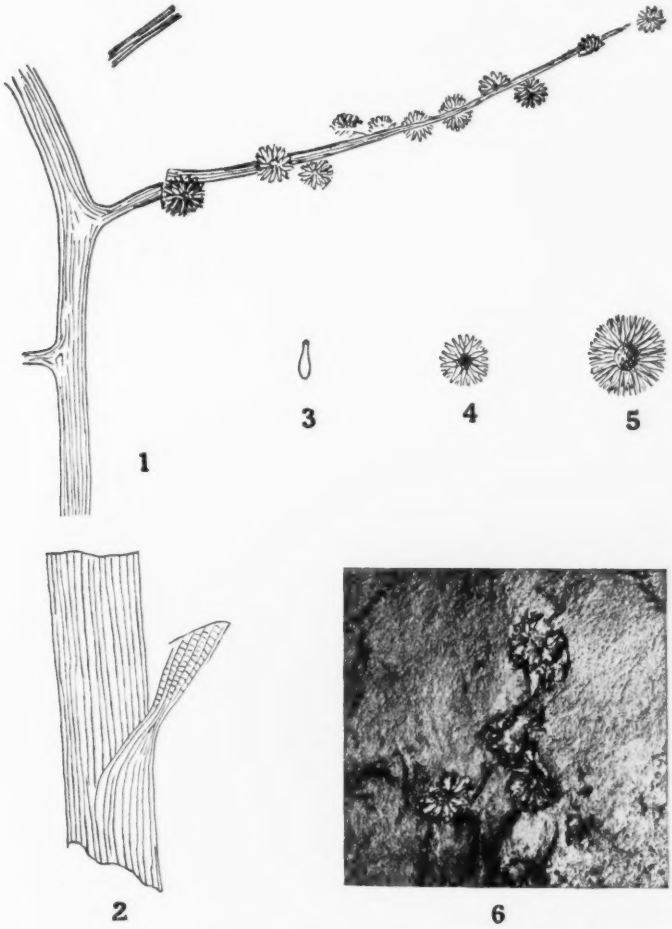
There can be no doubt but that these objects are the same as those from the Green River beds which NEWBERRY thought represented *Brasenia*, for in those Wind River specimens where the details are indifferently preserved the two cannot be distinguished, and the supporting stems and branches also are identical. The better preserved of these Wind River specimens show that they cannot represent *Brasenia*, since in that genus the fruiting heads are made up of a much smaller number of unsymmetrical carpels. The only modern forms known to the writer which have fruit heads like the fossil are those of *Sparganium*, and in this genus the individual fruits are also very like those of the fossil, consisting of numerous one-celled, nutlike fruits.

Associated with these *Sparganium*-like fruits are leaves of *Pontederites hesperia* Knowlton. These are neither common nor well preserved, but they show the unmistakable parallel veining with the transverse nervilles of that form, and they are too wide and otherwise dissimilar to be confused with the associated fragments of palm foliage, nor are they at all similar to the associated fragments of the problematical monocotyledon which has been called *Musophyllum*.

In one specimen a considerable fragment of a parallel veined stem, about 1.25 cm. in diameter, as flattened in the rocks, bears a fragment of a leaf with parallel veins and transverse veinlets exactly like *Pontederites hesperia*. This shows that the leaf was not petiolate nor auriculate at the base, but cuneate-lanceolate, narrowing at the base and then expanding to form a decurrent sheath, and that the leaves were alternate in arrangement.

This leaf-bearing stem fragment is marked by parallel veins exactly like the somewhat smaller branched stems which bear the fruit heads, and is identical with them in every respect, so that the conclusion is inevitable that both represent the same plant. This

conclusion receives corroboration, if such is deemed necessary, by their close association in the Wind River basin and by the presence of identical detached leaf fragments and fruit heads in the



FIGS. 1–6.—Fig. 1, specimen showing part of inflorescence with attached fruit heads; fig. 2, part of large stem with part of attached leaf; fig. 3, single fruit; fig. 4, small fruit head; fig. 5, large fruit head; fig. 6, photograph of several fruit heads; all figures natural size except fig. 6, which is slightly enlarged.

Green River formation, none of these classes of remains being found singly at any other horizons.

Summarizing the argument, it may be noted that fragments of leaves identical with those named *Pontederites hesperia* are found attached to particular stems; identical stems have attached to their lateral branches fruit heads like those named *Brasenia* (?) *antiqua*.

The family Pontederiaceae has petiolate, auriculate leaves, and the fruit is a single seeded utricle or a capsule; hence the fossil cannot be referred to that family. The family Alismaceae, which has leaves with a somewhat similar venation, has these leaves petiolate and frequently auriculate, and the fruits are conspicuously different, being achenes with markedly curved seeds. The only family that appears to fulfil the requirements of the fossils, so far as the latter are known, is the Sparganiaceae.

It is true that the leaflike spathes of the modern species have not been seen in the fossil material, a matter of lack of preservation of a minor detail, but in other respects the resemblance is most exact as to stem, inflorescence, fruit heads, and individual fruits. If the fossil leaves were narrowed and elongated, a most easily accomplished modification, they would be exactly like those of the modern species. I therefore propose that these fossils be referred to a single botanical species of *Sparganium*, of which I have attempted the restoration (fig. 7), and that this species be called

Sparganium antiquum (Newberry).—Plants of considerable size, at least 40 cm. tall, with stout, erect, parallel veined stems, with a few alternate sheathing leaves. Leaves broadly lanceolate, with numerous, essentially parallel, longitudinal veins, becoming crowded toward the base where they unite to form a not very conspicuous midvein, which, traced distad, becomes indistinguishable from the other veins in the upper half of the leaf. These veins are conspicuously connected by transverse veinlets which die out in the leaf sheaths, which later merge proximad with the stems, from which they are indistinguishable in appearance. The inflorescence is large and branched, fragments showing three lateral branches are preserved. These branches are at nearly right angles to the stem, rather stiff and curved, and bear from eight to ten nearly sessile

heads at somewhat irregular intervals, and progressively diminishing in size outward. It is not possible to determine whether or not the distal heads were staminate, as in the recent species of *Sparganium*, since the details of organization are not uniformly well preserved.

The material upon which this species is based is associated with an extensive warm temperate flora of a humid environment, and comes from Tipperary, Fremont County, Wyoming.

The family Sparganiaceae comprises the single genus *Sparganium* with ten or a dozen existing species, widely distributed in temperate and cool regions, growing in wet, or in some cases, submerged situations. They are chiefly confined to the Arctogaeic realm, but occur

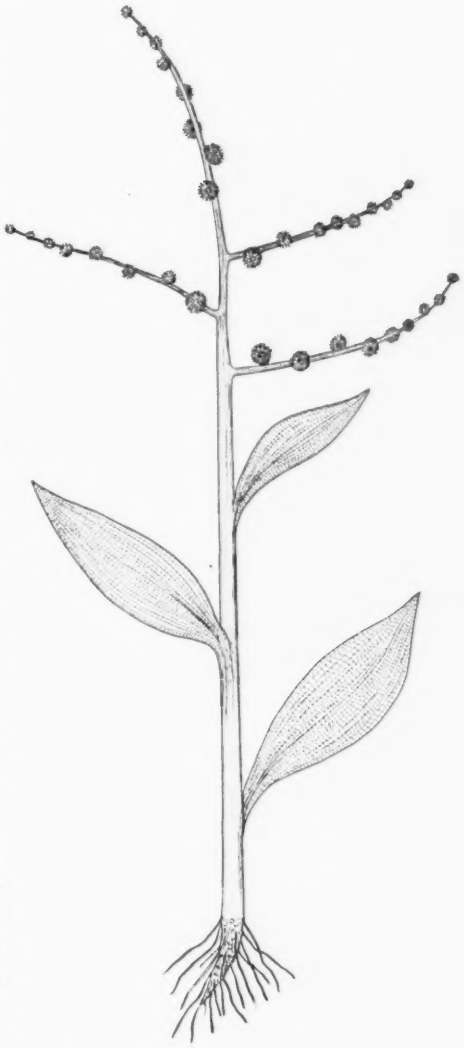


FIG. 7.—Restoration of *Sparganium antiquum* (Newberry); about ⅓ natural size.

also in Australia and New Zealand. The five or six North American species have a collective range from Newfoundland to British Columbia, and southward to Florida, Louisiana, and California. The discontinuous distribution of the genus in existing floras indicates a considerable antiquity, and this is fully borne out by the geological record.

Fossil remains that have been referred to *Sparganium* are fairly numerous in the rocks. Disregarding in the present connection the presence of several existing species in the Pleistocene deposits of both Europe and America, there are about fifteen extinct species that have been referred to this genus. The oldest of these are some not very convincing fruit heads from the Upper Cretaceous Atane beds of western Greenland,[3] and similar inconclusive remains from the Vermejo formation of Colorado.[4] The Eocene has furnished one or two species in addition to the one described in the present contribution. These occur in the early Eocene Fort Union formation of Montana,[5] and in the late Eocene, or possibly Oligocene of western Greenland,[6] Spitzbergen,[7] and Iceland.[8] The genus makes its appearance in Europe during Oligocene times, when it is reported to the extent of five species in beds of that age in France, Italy, Germany, and Alsace. Seven Miocene species have been recorded from the following countries: Switzerland, France, Syria, Croatia, Bohemia, Baden, and Transylvania. The Pliocene records comprise those of three species in Italy, France, Germany, and Holland.

[3] HEER, O., Fl. Foss. Arct. **3**:105. *pl. 28. fig. 12.* 1874.

[4] KNOWLTON, F. H., U.S. Geol. Survey Prof. Paper **101**:253. *pl. 32. fig. 6.* 1918.

[5] WARD, L. F., *Idem*, Bull. **37**:18. *pl. 3. figs. 6, 7.* 1887.

[6] HEER, O., Fl. Foss. Arct. **1**:97. *pl. 45. fig. 2.* 1868: *Idem*, **2**:467. *pl. 42. figs. 4, 5.* 1871.

[7] ———, *Idem*, **2**:51. *pl. 7. fig. 3c.* 1870.

[8] ———, *Idem*, **1**:145. *pl. 25. fig. 1.* 1868.

CLADOSPORIUM FULVUM

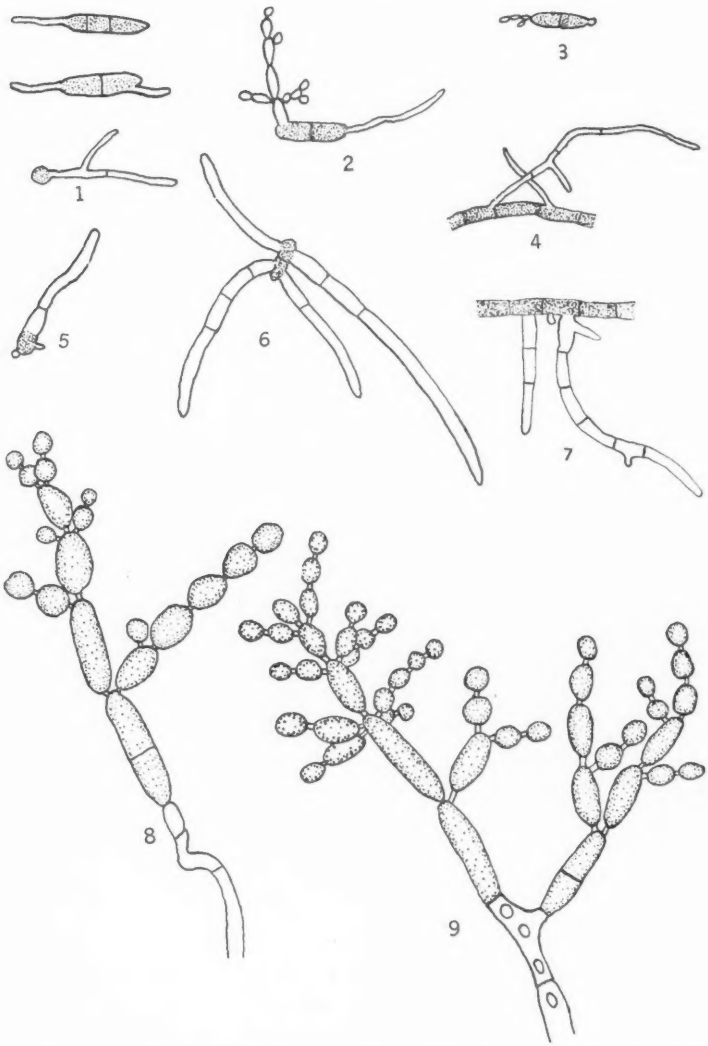
R. C. SPANGLER

(WITH NINE FIGURES)

Cladosporium fulvum Cke. has been observed in the United States since 1883. Although many workers have described it, MAKEMSON (**4**) was the first to publish an account of its life cycle. During the spring of 1915 this fungus caused much damage to the tomato plants in the greenhouses of the West Virginia Experiment Station. An investigation of the fungus was assigned to the writer by Dr. JOHN L. SHELDON, under whose directions the work was conducted.

When pure cultures of the fungus were examined, many small, almost spherical spores were found, besides the two-celled ones typical of *Cladosporium fulvum*. Both kinds of spores were placed in a hanging drop of sterile water, and in a few hours were germinating. The germ tubes, which were not more than one-fourth the diameter of the large spores, grew rapidly, branched, and became septate (fig. 1). Sometimes short chains of spores developed immediately from the old ones (figs. 2, 3). Probably this occurred only when the germinating spores were near the surface of the water, and the germ tubes started immediately into the air. Cells of the old mycelium also germinated in the same manner as the spores (fig. 4).

A hanging drop of culture medium was prepared and inoculated. Such cultures were kept in good condition for several months. At the end of four hours the spores were beginning to germinate. These germ tubes were about the same diameter as the spores and the mycelial hyphae (figs. 5–7). A mass of much branched, septate mycelium soon developed from each spore. In three days from the time the culture slides were prepared there were many branching conidiophores with chains of fully developed spores. One-celled spherical, and one-celled, two-celled, and occasionally three-celled elliptical spores were produced on the same conidiophore (figs. 8, 9).



FIGS. 1–9.—Fig. 1, germination of spores in water; fig. 2, formation of conidiospore directly from germinating spore; fig. 3, formation of spores directly from germinating spore; fig. 4, germination of cells of old mycelium in water; figs. 5–7, germination of spores and cells of old mycelium in culture medium; figs. 8, 9, conidiophores and spores (drawn from culture slide); ×1700.

Sometimes as many as six chains of the small oval to spherical spores developed from a large elliptical spore. Small isthmi connected the spores, which apparently developed on all the hyphae as soon as they reached the air.

Sometimes a germinating spore produced a short hypha on which small spores formed directly (fig. 2). The small spherical spores produced mycelium and conidiophores with all the different forms of conidia, just the same as the large two-celled spores and old mycelium. The age of the spores made considerable difference in the time of germination. New spores germinated in four hours, while those eight months old germinated in twenty-four hours. The spores retained their vitality at low and changeable temperatures, as well as at room temperature. They germinated readily after being kept outside in a dry condition from January 4 until May 1. The lowest temperature during this time was $-20°$ C.

Besides growing on the different kinds of culture media, the fungus grew just as well on corn meal that had been moistened and sterilized. Some spores were put on leaves of corn in the greenhouse, and the fungus developed on the leaves that were partially dead. When these leaves were placed in a moist chamber the growth was much more extensive. It also grew and produced spores on tomato leaves removed from the plant and placed in a moist chamber.

These data indicate that *Cladosporium fulvum* is a saprophyte which grows on living plants only when they are placed under abnormal conditions. MAKEMSON says that *C. fulvum* has "ability to exist as a saprophyte. Its growth on culture media is easily obtained even on sterilized filter paper where it grows and produces spores." DUGGAR (2) says that "under abnormal conditions, such as forcing and poor ventilation, many fungi are able to gain entrance and become the cause of epidemics, whereas, under more normal conditions, they remain as harmless inhabitants of dead material." *C. cucumerinum* is supposed to be parasitic only occasionally; *C. herbarum* was thought formerly to be wholly saprophytic; most of the other members of this genus are saprophytes (2).

It has been thought for several years that *Cladosporium* and *Hormodendron* are intimately connected (5). In 1910 BANCROFT (1)

stated that the life cycle of a fungus that he had been studying was composed of the two conidial forms, *Cladosporium* and *Hormodendron*, and that the former was a late saprophytic form on dead leaves that had previously been attacked by the latter. MASSEE (**5**) says that *Cladosporium epiphyllum* and *Hormodendron Hordei* are different conidial stages of the same fungus. STEVENS (**6**) gives *H. herbarum* and *H. cladosporioides* as two conidial stages of *Mycosphaerella tulasnei* JANCZ (**3**).

From what has been discovered in this investigation, it seems certain that *Cladosporium* and *Hormodendron* are one and the same fungus. The one-celled spores near the tip characterize the fungus as *Hormodendron*, while the two-celled spores, after the unicellular ones have fallen off, indicate that this organism is a species of *Cladosporium*. It is probable that these fungi do not possess two types of conidia, but that the two-celled bodies confused as spores are fragments of modified conidiophores. This theory is strengthened by the fact that even unicellular and bicellular pieces of hyphae germinated and reproduced just as typically as the so-called two-celled spores.

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1. BANCROFT, C. K., Relationship between *Cladiosporium* and *Hormodendron*. Ann. Botany **24**:359–372. 1910.
2. DUGGAR, B. M., Fungous diseases of plants. 1909.
3. JANCZEWSKI, E., Bull. Acad. Sci. Cracow. 1892, 1893, 1894.
4. MAKEMSON, W. K., The leaf mold of tomatoes, caused by *Cladosporium fulvum* Cke. Mich. Acad. Sci. R. 1918.
5. MASSEE, GEO., Diseases of cultivated plants and trees. 1910.
6. STEVENS, F. L., The fungi which cause plant diseases. 1913.

BRIEFER ARTICLES

THE PROPHYLLUM OF GRASSES

(WITH ONE FIGURE)

In a recent article Mrs. ARBER[1] discusses the nature of the prophyllum of grasses, and confirms the position taken by BUGNON that this organ represents a single leaf. The evidence adduced in support of this view may be summarized as follows: (1) the two prophyllary fibrovascular bundles that coincide more or less closely with the two keels are of unequal size; (2) the large bundle occupies a position opposite the median bundle of the next succeeding leaf; (3) as a result of mechanical pressure the prophyllary bundles are not always located in the keels.

According to BUGNON, the smaller prophyllary bundle is a lateral of the first. None of these arguments appears convincing to the writer. If the two bundles in the prophyllum were exactly equal it might indicate a double organ, but inequality can scarcely be said to be incompatible with the idea that two leaves are represented. Is it improbable that two congenitally fused organs, although of the same origin, should have an unequal development? Likewise, the position of the larger bundle opposite the median bundle of the next leaf would seem of little weight, unless it can be shown definitely that the smaller bundle occupies a higher position on the axis.

That the keels in a large measure are the result of mechanical pressure is evident, and that a displacement of the bundle should result seems not improbable. It is not clear, however, how this displacement indicates that both bundles belong to a single leaf.

Opposed to such arguments is the very direct evidence of dual origin afforded by the not infrequent formation of two buds in the axil of the prophyllum of maize.

A type of maize from the Mexican plateau normally produces branches in the axils of the prophylla of the ear stalks, and in certain strains as high as 5 per cent of the individuals afford instances of two buds from the same prophyllum. These prophyllary buds are not mere rudiments, but develop into secondary ears of approximately equal size.

[1] ARBER, AGNES, Leaves of the Gramineae. BOT. GAZ. **76**:374–388. 1923.

Prophyllary branches also occur regularly in teosinte (*Euchlaena mexicana*), and cases of two prophyllary branches have been observed in the second generation of a hybrid between maize and teosinte (fig. 1).

When a single bud develops in the axil of a prophyllum it always stands adjacent to one of the keels. No doubt mechanical pressure might displace a bud from its normal position, but mechanical pressure

FIG. 1.—Dorsal view of branch of *Euchlaena*×*Zea* hybrid, showing two secondary branches in axil of prophyllum.

would scarcely explain the formation of a second bud. Fusion of adjacent leaves is not infrequent, and there are many examples in aberrant types of maize. In fact, fusion of the leaves usually accompanies extreme shortening of internodes.

It seems more reasonable to suppose that the prophyllum represents two leaves than that two buds should develop in the axil of a single leaf.—G. N. COLLINS, *Bureau of Plant Industry, Washington, D.C.*

CURRENT LITERATURE

BOOK REVIEWS

Electrophysiology of plants

The field of electrical response in plants has been summarized by STERN,[1] as the fourth volume of the series of monographs from the field of physiology of plants and animals published by SPRINGER. The book contains nine chapters, the first of which considers the physical basis of electrophysiology of plants, and the ways in which various forms of energy may be converted into electrical energy in the cell, and how in turn the electrical energy may be converted into mechanical, osmotic, and chemical energy.

The second chapter deals with the effects of electric currents, physical and vital, upon the protoplasm and cell. Electrophoresis, electric osmose, and concentration changes due to electrical phenomena are explained in some detail. Then follow chapters on the quantitative relations between stimulation and response, electrotaxis, electrotropism, and electronasty. These subjects possibly receive more attention than their relative importance would justify, but research has been more general in the field of responses of directly visible kind.

The seventh chapter discusses the influence of electricity on developmental processes and metabolism of plants, and here one wishes that much more information were available. The final chapters deal with the production of electrical energy by the plant, and the problems and tasks of electrophysiological research of the future.

About 200 literature citations are given at the close, arranged in accordance with the various chapter headings. This little volume is interestingly written, and will prove helpful to anyone who desires to obtain a general view of this special field of plant physiology, as well as to the more serious student who may care to investigate the problems of immediate response of living cells to electrical conditions, or the more important developmental and metabolic consequences of the electrical conditions surrounding or pervading the living cells of the organism.—C. A. SHULL.

MINOR NOTICES

Flora Balearica

KNOCHE[2] has completed his discussion of the flora of the Balearic Isles by adding to the volumes already noted[3] one containing a discussion of the floristic and ecological problems, and another of plates illustrating about 50 species

[1] STERN, KURT, Elektrophysiologie der Pflanzen. 8vo., pp. viii+219. figs. 32. Berlin: Julius Springer. 1924.

[2] KNOCHE, HERMAN, Flora Balearica. Étude phytogéographique sur les Isles Baléares. Montpelier. 8vo. **3** and **4**:XV+411. *pls. 1–47*. 1923.

[3] BOT. GAZ. **75**:324–325. 1923.

and varieties from the flora, and showing characteristic views of the vegetation of the islands. In sketching the geologic history of this portion of the Mediterranean region, there is postulated a continent in the Eocene stretching from New Zealand through America to the Balearics. The lost continent of Atlantis is also regarded as an established fact, and is called upon to further explain certain affinities. Many of the typical sclerophylls of the Mediterranean, such as *Myetus*, *Pistacia*, *Rhamnus*, *Buxus*, and *Laurus* are referred to an Eocene origin, with affinities to forms in New Zealand, Chili, Mexico, and California, as well as with the remainder of the Mediterranean floras. The vascular endemics number 61 species, and such groups as relic, recent, Tyrrhenian, and Mediterranean are recognized.

The principal plant association type is an open scrub or "garigue," in which the dominant species are *Pistacia lenticus*, *Cistus alba*, *C. monspeliensis*, *Rosmarius officinalis*, and *Olea silvestris*.—GEO. D. FULLER.

Forestry almanac

A small volume[4] compiled and issued by the American Tree Association, of which CHARLES LATHROP PACK is president, contains information of interest to botanists regarding the forests of our land. Among the subjects included are the history and organization of the United States Forest Service, details regarding various forestry associations now existing throughout the country, and a list of universities and colleges offering educational courses in forestry. The forest taxation laws of various states are summarized, and forest statistics for the different states are presented. In addition there are data regarding the forests of Alaska, Hawaii, Guam, Samoa, and Canada, making it a convenient and indispensable source of information for all who are interested in the present condition of forests in North America and in our possessions beyond the seas.—GEO. D. FULLER.

NOTES FOR STUDENTS

Vegetation of middle west.—Recent publications have tended to clarify our understanding of the grassland region that occupies the center of our continent. GLEASON[5] holds that these grasslands probably date back to the changes of climate that resulted from the Cretaceous uplift of the Rocky Mountain system, when increasing aridity caused the retreat of forest vegetation. During the Tertiary this grassland flora was probably further differentiated from the elements centering in the Appalachian Mountains, in the Mississippi Embayment, in the Ozark Mountains, in the plains of Kansas and Nebraska, and in eastern Canada. During the various glacial and interglacial

[4] American Tree Association. Forestry Almanac. viii+225. Philadelphia: J. B. Lippincott Co. $2.00.

[5] GLEASON, H. A., The vegetational history of the middle west. Ann. Assn. Amer. Geog. **12**:39–85. 1923.

periods fluctuations in its extent have taken place, but it is believed that the occupancy of the Ohio Valley by deciduous forests has been continuous. During the Sangamon interglacial period there seems to have been a considerable western extension of deciduous forests, while during the Wisconsin glaciation a semi-arid climate dominated the region, and was succeeded by a xerothermic period following the retreat of the ice, and causing the invasions of western Ohio by prairies. Increased precipitation then caused the westward migration of forests to be met and combated by the arrival of the Indian and the accompanying prairie fires. During the nineteenth century afforestation again seems to have continued until checked by cultivation.

In the analysis of existing conditions, KINCER[6] has carefully discussed the moisture and temperature conditions in relation to both natural vegetation and crop production. In a closely related discussion, MARBUT,[7] postulating the general uniformity of mature soils, whatever the nature of the parent material, throughout any given climate and vegetational area, shows a remarkable agreement between the rainfall regions and the belts of black, dark brown, and brown soils that run from north to south. He has also shown a zone of alkaline salt accumulation, usually lime carbonate, to be characteristic of the mature soils of the middle west, the carbonate layer approaching the surface in the more arid west, but retreating downward and finally disappearing in the humid east.

As a fitting climax to this series of articles, SHANTZ[8] has described the vegetation of the plains region, relating it to both soil and climate. The chief types of grassland distinguished, described, and mapped are short grass, tall grass, mesquit and desert grass, savanna, sage brush, and mesquite grass. Subdivisions of these types are recognized, and the resulting map is a very decided contribution to our knowledge of the vegetation of the middle west.

The interrelations of vegetation, soil, and climate have an emphasis seldom given. Thus the habitat may be evaluated either by the interpretation of the vegetation or by the interpretation of the soil profile. With no vegetation there would have been no carbonate layer, while the carbonate layer in its turn materially affects the character of the vegetation. Sand equalizes habitats by affording the best conservation of moisture in arid regions and the best drainage in humid climates.—GEO. D. FULLER.

Taxonomic notes.—BALL[9] has issued a separate of his presentation of the Salicaceae of the Pacific States. Each species is illustrated, helping materially

[6] KINCER, J. B., The climate of the great plains as a factor in their utilization. Ann. Assn. Amer. Geog. **13**:67–80. 1923.

[7] MARBUT, C. F., Soils of the great plains. Ann. Assn. Amer. Geog. **13**:41–66. 1923.

[8] SHANTZ, H. L., The natural vegetation of the great plains region. Ann. Assn. Amer. Geog. **13**:81–107. 1923.

[9] BALL, C. R., The willows of the Pacific States. Reprinted from *Illustrated Flora of the Pacific States*. pp. 486–507. 1923.

in determination in this difficult group. *Populus* is represented by 4 species, and *Salix* by 46, 6 of which are credited to the author. BALL[10] has also published a new variety of *Salix discolor* from South Dakota, and announced extension of range of five other species.

BLAKE[11] has published the results of his study of the Asteraceae as represented in the National Herbarium, supplemented by material in the Gray Herbarium, the herbarium of the Field Museum, and the herbarium of the New York Botanical Garden. The work includes Mexico and South America, especially the northern and western portions of the latter. The nine tribes presented include 118 new species, distributed among 45 genera, the largest numbers occurring in *Perymenium* (19), *Clibadium* (9), *Zexmema* (9), *Verbesina* (9), and *Hieracium* (8). One new genus (*Trichocoryne*) of the Helenieae is established.

HITCHCOCK[12] has published a monograph of the North American species of *Aristida*, recognizing 60 species, 7 of which are described as new. The descriptions are very complete, and include detailed lists of all collections of material. The new species are chiefly from the West Indies, with one from Florida, and one from Lower California.

RYDBERG,[13] in continuation of his studies of North American Fabaceae, has presented 17 genera of Galegeae, including a new genus (*Sauvallella*) based on *Corynella immarginata* Wright.

TIFFANY[14] has described five new species of *Oedogonium* and one new species of *Spirogyra*, based on collections from Iowa and Ohio.—J. M. C.

Nitrogen fixation by green algae.—Several years ago WANN[15] reported the fixation of free nitrogen by seven species of algae belonging to the Chlorophyceae. The claim that wheat plants have power to fix free nitrogen was made at about the same time by LIPMAN and TAYLOR.[16] The problem of fixation of nitrogen by green algae has been reexamined critically by BRISTOL and PAGE,[17] who have used the same nutritive conditions as WANN employed, but more accurate methods of analysis for nitrogen in the presence of nitrates, namely,

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[10] BALL, C. R., Extension of range and a new variety in *Salix*. Rhodora **26**:135–144. 1924.

[11] BLAKE, S. F., New American Asteraceae. Contrib. U.S. Nat. Herb. **22**:587–661. *pls. 54–63*. 1924.

[12] HITCHCOCK, A. S., The North American species of *Aristida*. Contrib. U.S. Nat. Herb. **22**:517–586. 1924.

[13] RYDBERG, P. A., Genera of North American Fabaceae II. Tribe Galegeae. Amer. Jour. Bot. **11**:470–482. *pls. 33–36*. 1924.

[14] TIFFANY, L. H., Some new forms of *Spirogyra* and *Oedogonium*. Ohio Jour. Sci. **34**:180–187. *pls. 3*. 1924.

[15] BOT. GAZ. **73**:247–248. 1922.

[16] LIPMAN, G. B., and TAYLOR, J. K., Proof of the power of the wheat plant to fix atmospheric nitrogen. Science N.S. **56**:605–606. 1922.

[17] BRISTOL, B. MURIEL, and PAGE, H. J., A critical inquiry into the alleged fixation of nitrogen by green algae. Ann. Applied Biol. **10**:378–408. 1923.

the Ulsch in combination with the Kjeldahl method, to avoid the destruction of nitric acid while boiling in the presence of sulphuric acid. This source of error in WANN's work is shown to represent 5–14 per cent of the nitrate present in the culture medium.

Four genera of algae are represented in BRISTOL and PAGE's work, *Chlorella*, *Pleurococcus*, *Cystococcus*, and *Scenedesmus*. The recovery of nitrogen from the cultures by their methods of analytical procedure was 99.28 per cent. and from the controls 99.25 per cent. The authors have failed entirely to corroborate WANN's results. Their concluding sentence puts the case succinctly. "While it is quite conceivable that green algae might assimilate atmospheric nitrogen under certain conditions as yet unknown, there is so far no trustworthy evidence that they can do so."

In regard to the higher non-legumes, like wheat and other Gramineae, the burden of proof that they can assimilate free atmospheric nitrogen rests with those making the claim. The mere assertion that they do cannot be taken seriously until the statement is supported by convincing evidence obtained by methods that eliminate all sources of error. Such data at present are not available.—C. A. SHULL.

Insect pollination in Aristolochia.—This genus readily attracts attention because of the unusual shape of the flowers, and often by their bizarre coloring, large size, and unpleasant odor. In general the flowers consist of a basal bulb and an open flaring face connected by a long tube. In most species the face is strikingly colored and ornamented with radial lines converging at the mouth of the tube. This tube is lined with hinged hairs, while the bulb into which it expands possesses transparent spots or "windows" near its base. All these structures seem connected with a rather complicated system of insect-pollination. In order to understand this process more fully, PETCH[18] for several years has been examining these plants in the gardens at Peradeniya.

Of the twelve species investigated, self-pollination obtained in a few, but most were protogynous and dependent upon the visits of various flies for the transportation of pollen from flower to flower. In general the flowers open in the morning, and the insects attracted by the conspicuous face and the vile odor enter the tube, from which their escape is prevented by a lining of hinged hairs. Proceeding to the bulb, the light penetrating the thin tissues of the "windows" attracts them to the vicinity of the stigma and the stamens. The stigmas are receptive as soon as the flower opens, while the pollen is shed late in the day or during the ensuing night. In some flowers food for the insects is found within the bulb, but in nearly all the insects are not liberated until the morning of the second day, when the guardian hairs wilt, leaving a clear passage for the flies to traverse, after which many find their way to a new set of flowers. In promoting the migration the attracting odor usually persists for the first day only.

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[18] PETCH, T., Notes on *Aristolochia*. Ann. Roy. Bot. Gard. Peradeniya **8**: 1–108. 1924.

In addition to establishing the general behavior just summarized, the report contains an abundance of interesting details of the behavior of different species, and is illustrated by several good plates presenting the details of flower structure. There are also notes on the identity of the insect visitors.—GEO. D. FULLER.

Soil temperature in deserts.—The temperature of the surface soil in deserts is known to vary considerably, although exact data on the subject have been few. SINCLAIR[19] found near Tucson, Arizona, a daily range from 17.0° to 71.5° C. at a depth of 0.4 cm. During the same day the range at a depth of 10 cm. was but 26.3° to 40.1° C., and at 100 cm. there was a constant temperature of 24.5° C. throughout the day. At 4 cm. above surface the range was from 10° C. to 55.7° C.

A somewhat similar range was found by WILLIAMS[20] in a valley 12 miles southeast of Cairo, where during August, 1922, the surface of the sand had a daily temperature range of 37° C., with a weekly range of 17.5° to 58.2° C., while in the shade the variations were 21.2° to 35.9° C., and 12 m. within a cave from 24.0° to 25.4° C. only. The daily range of relative humidity was as high as from 14 to 80 per cent.

In Palestine BUXTON[21] found maximum surface temperatures ranging from 50° to 74° C. He discusses the technique of such surface measurements and the cause of very considerable variations within a very limited space.

From even these scanty data it is evident that desert vegetation has to contend both with very high surface temperatures, and with a wide temperature range for different parts of the same plant, and for different hours of the same day. While this has been known for many years, the investigations cited give some definite idea of the actual temperatures involved.—GEO. D. FULLER.

Alpine vegetation of Colorado.—HOLM[22] has recently discussed some 170 species of vascular plants collected in the alpine region of Colorado, and noted the occurrence of many of them in other lands. It was found that 63 species occur also in the Arctic regions, 31 are circumpolar, while of the remainder nearly 100 are endemic to North America, and many to these mountains. Four distinct elements of this vegetation are recognized: the circumpolar, the Arctic, the alpine, and the lowland. Examining the geographic distribution of these alpine plants in detail, the author finds many points that seem to support SCHOUW's hypothesis that the same species has developed at several stations far removed from one another.

The plates are filled with over seventy figures of natural size drawings of some of the more typical species.—GEO. D. FULLER.

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[19] SINCLAIR, J. G., Temperatures of the soil and air in a desert. Mo. Weath. Rev. 50:142–144. 1922.

[20] WILLIAMS, C. B, A short bioclimatic study in the Egyptian desert. Egypt Dept. Agric. Tech. and Sci. Service Bull. 19. pp. 20. 1923.

[21] BUXTON, P. A., The temperature of the surface of deserts. Jour. Ecol. 12:127–134. 1924.

[22] HOLM, THEODORE, The vegetation of the alpine region of the Rocky Mountains in Colorado. Mem. Nat. Acad. Sci. 19. pp. 45. 1923.